Chronoethological assessment of well-being and husbandry in captive koalas *Phascolarctos cinereus*, Goldfuss 1817

Dissertation
zur Erlangung des Doktorgrades
der Naturwissenschaften

vorgelegt beim Fachbereich Biowissenschaften
der Johann-Wolfgang-Goethe-Universität
in Frankfurt am Main

von
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aus Groß-Umstadt

Frankfurt, Februar 2007

vom Fachbereich FB 15 Biowissenschaften der
Johann-Wolfgang-Goethe-Universität als Dissertation angenommen

Dekan: ....

Gutachter: ....

Datum der Disputation: ....

For my mother, Andrea Benesch

In the heat of the day in an average zoo,
What's a koala most likely to do?
In the fork of a tree, in a featureless heap.
It closes its eyes and endevours to sleep.

And the visiting children and parents, they both
Say, "Oh, what a lazy marsupial sloth!
It's far to lethargic to romp or to toil,
Perhaps it is drunk on the eukalypt oil."

But that isn't fair; it's improper to mock
A creature that works on a different clock.
The schedule koalas are destined to keep
Is to deal with their business while we are asleep.

And, up in the treetops, throughout the long night,
They climb and they feed and make love, or they fight.
And if they took notice of me or of you,
They'd probably think we're a sluggardly crew.

Ronald Strahan, "The Incomplete Book
of Australian Mammals"

Contents

Chronoethologische Validierung des Wohlbefinden und der Haltung von Koalas *Phascolarctos cinereus*, Goldfuss 1817 in Zoologischen Gärten

Einleitung

Das Leben aller Organismen ist rhythmisch organisiert. Die grundlegenden Rhythmen werden endogen durch ein Multioszillatorensystem aus inneren Uhren erzeugt. Viele davon sind circadian, dauern also ungefähr 24 Stunden. Da es in einem Organismus eine Vielzahl von circadianen Rhythmen (z.B. Schlaf-Wach-Rhythmus, Körpertemperatur, Hormonspiegel) gibt, müssen diese miteinander und mit der Umwelt synchronisiert werden. Dies geschieht durch sogenannte Zeitgeber, rhythmisch auftretende, externe Signale. Der wichtigste externe Rhythmus ist der Tag-Nacht-Wechsel und so ist es nicht verwunderlich, daß Sonnenlicht als einer der stärksten Zeitgeber wirkt.

In einer künstlichen Umgebung erreichen Zeitgeber häufig nicht die notwendige Stärke, um den Organismus zu synchronisieren. Die Folge ist eine Abkopplung der endogenen Rhythmen von ihrer Umwelt und von einander. Eine interne Desynchronisation (z.B. ein Jetlag) ist die Folge. Zudem können andere Signale direkt auf den Organismus einwirken und die endogenen Rhythmen überlagen. Man spricht hier von einer Maskierung. Solche Veränderungen können zu Unwohlsein führen und sollten vermieden werden.

Andererseits ist es möglich, daß der physiologische Zustand des Tieres, z.B. Östrus, Krankheit oder Stress, Einfluss auf den circadianen Rhythmus hat. In diesem Fall kann die Beobachtung des entsprechenden Parameters (z.B. Aktivitätsrhythmus) Aufschluss über den Zustand des Tieres geben.

Koalas sind beliebte Zootiere, doch ihre Haltung ist problematisch. Neben ihrer Spezialisierung auf Eukalyptusblätter als einzige Nahrung gelten sie als anfällig für "Stress" und Krankheiten. Aus diesem Grund hat insbesondere in europäischen Zoos die Überwachung ihres Wohlbefindens eine hohe Priorität. Stressoren werden nach Möglichkeit ausgeschlossen. Stresssignale bei Koalas sind jedoch eher vage, und traditionelle Kontrollmethoden wie regelmäßiges Wiegen können selbst als Störung auf den Koala wirken und so das Wohlbefinden vermindern. Zudem werden Tagesabläufe in der Haltung dem Zeitplan des Tierpflegers, nicht dem endogenen Rhythmus des Koalas angepaßt.

Eine chronoethologische Untersuchung der Aktivitätsmuster von Koalas in Zoohaltung könnte Informationen über die grundlegenden circadianen Rhythmen geben. In dieser Studie wurden die einwirkenden externen Faktoren darauf untersucht, inwieweit sie als Zeitgeber oder Maskierung wirken. Es wurde zudem versucht, den Tagesablauf stärker an die Bedürfnisser der Koalas anzupassen.

Methode

In drei Zoologischen Gärten in Australien und Europa wurden die circadianen Rhythmen für allgemeine Aktivität, Futteraufnahme und lokomotorische Aktivität untersucht. Dazu wurden insgesamt 17 Koalas unter vier Haltungsbedingungen mit 24-Stunden-Zeitraffer-Video aufgezeichnet:

Taronga Zoo, Sydney liegt innerhalb des natürlichen Verbreitungsgebietes der Koalas. Die Tiere werden in Außengehegen gehalten und sind dem natürlichen Klima und den natürlichen Schwankungen der Tageslängen ausgesetzt. Futter wird täglich in der Umgebung von Sydney gesammelt.

Koala Walkabout: Vier Koalas (ein Männchen, drei Weibchen) wurden 2004 über einen Zeitraum von einem Jahr beobachtet. Im Sommer 2003/04 wechselte die Gruppenzusammensetzung aufgrund von Zuchtbemühungen. Daher wurden drei weitere Weibchen für jeweils einige Wochen beobachtet. Die Tagesroutine beinhaltet die morgendliche Gehegereinigung um 07:00 und die Fütterung um 15:30. Kontakt mit dem Pfleger ist selten. Im Verlauf dieser Studie wurden die Tiere in einem Abstand von einem bis vier Monaten gefangen, gewogen und bei den Weibchen der Beutel auf Jungtiere kontrolliert.

Koala Encounter: Vier adulte Weibchen und ein einjähriges Jungtier wurden für sechs Wochen im Sommer 2005 (Dezember-Januar) beobachtet. Die Tiere wurden in zwei Gruppen gehalten. An den meisten Tagen betreten Besucher für zwei Stunden das Gehege, um sich neben den Koalas photographieren zu lassen. Kontakt mit den Tieren ist verboten und ein Pfleger überwacht den Zustand der Tiere optisch. Stresssymptome werden nur selten beobachtet. Die Koalas werden dreimal täglich gefüttert (07:00, 11:00 und 13:00), dabei kommt es zu gelegentlichem Kontakt mit den Pflegern. Normalerweise werden die Koalas alle zwei Wochen gewogen, dies fand jedoch nicht während der Beobachtungszeit statt.

In den beiden europäischen Zoos werden die Koalas in klimatisierten Innengehegen gehalten. Zusätzlich zu einem Glasdach werden die Gehege künstlich beleuchtet. Im

Winter wird der Tag dadurch um mehrere Stunden verlängert. Die Koalas sind durch eine an der Decke offene Glaswand nach Geschlechtern getrennt, können sich aber sehen, hören und riechen. Kontakt findet nur kontrolliert zu Paarungsversuchen statt. Futter wird zweimal wöchentlich von Plantagen in Südengland bzw. Florida eingeflogen.

Zoo Duisburg: Ein Männchen und drei adulte Weibchen wurden für je sechs Wochen im Sommer 2003 (Juni-Juli) und im Winter 2003 (November-Dezember) beobachtet. Die Tiere haben unregelmäßigen Kontakt zum Pfleger. Im Laufe des Vormittags werden die Gehege gereinigt und zu unterschiedlichen Zeiten Futter ausgegeben. Zweimal die Woche werden die Tiere gewogen.

Tiergarten Schönbrunn, Wien: Ein Männchen und ein Weibchen wurden für je sechs Wochen im Sommer 2004 (Juni-Juli) und im Winter 2004/05 (Dezember-Januar) beobachtet. Die Gehege werden am frühen Morgen gereinigt, wobei es fast täglich zu Kontakt zwischen Pfleger und Koala kommt. Täglich um 10:15 wurden die Tiere gewogen und gefüttert. Aufgrund der Ergebnisse dieser Studie wurde im Juni 2005 das Wiegen auf 16:00 verschoben und die Tiere wurden für weitere sechs Wochen beobachtet.

Die Videoaufzeichnungen wurden in bezug auf das Verhaltensmuster und die Reaktion auf verschiedene Pflegetätigkeiten analysiert. Zusätzlich zu den Aktivitätsmustern wurden Zeitbudget und Tag:Nacht-Ratio des Verhaltens berechnet.

Ergebnisse

Die Koalas im Koala Walkabout, Sydney, zeigten ein einheitliches Aktivitätsmuster, welches deutlich durch das natürliche Licht entrained wurde. Während der Nacht war die Aktivität höher, und es konnte eine ausgeprägte Ruheperiode am Morgen beobachtet werden. Zu dieser Zeit stellten Degabriele and Dawson (1979) bei Koalas eine physiologisch niedrigere Körpertemperatur fest als zu anderen Tageszeiten. Aktivitätsmaxima standen in Bezug zur Dämmerung und veränderten sich im Laufe des Jahres in Relation zur Tageslänge. Zusätzlich zeigte sich ein deutlicher Einfluß der nachmittäglichen Fütterung, die durch ein hohes Aktivitätsmaximum begleitet wurde. Mit kürzer werdenden Tagen kam es zu einer Überlappung des Stimulus Fütterung mit dem Stimulus Abenddämmerung. Bei drei Koalas verschwand die Aktivitätsphase in der Abenddämmerung zugunsten der Fütterung, doch ein Weibchen fraß nur noch in der Abenddämmerung.

Die Aktivitätsmuster in den Zoos Duisburg und Wien variierten deutlich zwischen den Individuen. In einigen Fällen fehlte ein erkennbarer Rhythmus, insbesondere der in Sydney deutliche Unterschied zwischen Tag und Nacht. Obwohl die Aktivitätsmaxima in

Relation zum Licht standen, war das Entrainment durch das durch das Dach einfallende Sonnenlicht eher schwach. Im Winter reagierten die Koalas primär auf die künstliche Beleuchtung, einige Individuen jedoch zeigten zusätzliche Aktivitätsmaxima in Relation zum Sonnenlicht. Die Aktivitätsmuster dieser Koalas waren weniger stark strukturiert und unterschieden sich drastisch von den Mustern, die in der Literatur bei freilebenden Koalas beschrieben wurden. Aktivität stand häufig in Relation zu der Anwesenheit des Pflegers und dem Einbringen neuen Futters. Die Dauer und der Abstand einzelner Aktivitäts- und Fressperioden waren im Zoo Wien waren deutlich kürzer als in den beiden anderen Zoos. Insbesondere das Weibchen fiel durch die hohe Frequenz im Wechsel zwischen Ruhe und Aktivität auf.

Das Zeitbudget der Koalas im Koala Walkabout, Zoo Duisburg und Zoo Wien lag innerhalb des für freilebende Koalas bekannten Bereichs. Die Koalas ruhten zwischen 74,1 und 81,7% der Zeit, wobei es keine eindeutigen Unterschiede zwischen den Geschlechtern und nur wenige Unterschiede zwischen den Zoos gab. Fressen war mit 10,7 bis 17,3% die häufigste Aktivität; die Koalas in Duisburg fraßen am längsten. Die Dauer des Fressens war im Winter sowie bei säugende Weibchen länger. Lokomotorische Aktivität zeigte deutliche Unterschiede zwischen den Zoos. Sie war am höchsten in Wien und am niedrigsten in Duisburg. Die Koalas kamen nur gelegentlich auf den Boden. Im Koala Walkabout war dies nötig, um zwischen einigen der Bäume zu wechseln. Daher wurden diese Koalas, insbesondere das Männchen, in bis zu 7% der Beobachtungsintervalle auf dem Boden beobachtet. In den beiden europäischen Zoos war es nicht notwendig, den Boden zu betreten. In Duisburg geschah dies auch selten. In Wien jedoch kamen die Koalas häufig auf den Boden, besonders das Weibchen, um das Gehege zu erkunden oder zu trinken.

Die Koalas waren nicht streng nachtaktiv, aber bei den meisten beobachteten Koalas fand ein größerer Teil der Aktivität während der Nacht statt. Dies war besonders ausgeprägt in dem Sydney Weibchen Yindi, die tagsüber kaum Aktivität zeigte. Das Duisburger Männchen und das Wiener Weibchen waren im Winter jedoch während des Tages etwas aktiver als während der Nacht.

Die Pfleger im Koala Walkabout, Sydney, hatten selten direkten Umgang mit den Koalas. In den wenigen Fällen, in denen die Tiere gefangen wurden, wehrten sie sich, sonst reagierten sie kaum auf den Pfleger. Nach dem Wiegen bzw. der Kontrolle des Beutels beruhigten sie sich jedoch schnell wieder. In den beiden europäischen Zoos hatten die Koalas regelmäßig Kontakt zu den Pflegern. In Duisburg zeigte sich kaum ein Einfluss auf das Verhalten und die Koalas setzten nach dem Wiegen zumeist ihre vorherige Tätigkeit

(Ruhen oder Fressen) fort. In Wien reagierten beide Tiere sehr stark auf den Pfleger. Die Morgenreinigung löste lokomotorische Aktivität im Weibchen aus. Das tägliche Wiegen um 10:15 fiel in die Ruhephase der Koalas. Während das Weibchen danach meist fraß, blieb das Männchen an den meisten Tagen inaktiv und begann seine eigentliche Futteraufnahme erst am Nachmittag.

Im Koala Walkabout fand die Fütterung am Nachmittag statt. Davor wurde erhöhte lokomotorische Aktivität beobachtet, und nach dem Füttern fraßen die Tiere für längere Zeit, mitunter für über eine Stunde. In den beiden europäischen Zoos wurde am Morgen gefüttert. Die dieser Fütterung folgenden Aktivitätsmaxima waren niedriger als die am Koala Walkabout und oft fraßen einzelne Tiere erst am Nachmittag. Vor der Fütterung wurde selten Aktivität beobachtet.

Die Aktivitätsmuster im Koala Encounter, Sydney, stimmten während der Nacht fast vollständig mit denen der Weibchen im Koala Walkabout überein. Tagsüber gab es jedoch dramatische Unterschiede. Während die Koalas im Walkabout am Morgen ruhen, zeigten sich im Encounter drei Aktivitätsmaxima, die mit Fütterungen in Verbindung standen. Die Koalas im Encounter waren insgesamt aktiver als die im Walkabout. Die lokomotorische Aktivität war ebenfalls erhöht und die Tiere waren häufiger auf dem Boden.

Im Koala Encounter wurden Phasen mit parallel erhöhter lokomotorischer Aktivität in zwei Tieren beobachtet. Dies geschah zum einen nachdem zwei Weibchen, Maggie und Carla, in ein gemeinsames Gehege transferiert wurden, und zum anderen bei Cooee und ihrer Tochter Coco, die zur Beobachtungszeit entwöhnt wurde.

Im Koala Walkabout und in Duisburg standen den Tieren lebende Nichteukalyptus-Bäume als Ruheplatz zur Verfügung. Diese wurden von einigen Koalas intensiv genutzt, insbesondere tagsüber. Zwei der Weibchen in Duisburg wurden allerdings sehr selten in den Bäumen beobachtet.

Diskussion

Die Beobachtungen aus dem Koala Walkabout zeigen, dass die Aktivität der Koalas durch zwei Faktoren beeinflusst wird. Sonnenlicht wirkt als Zeitgeber mit unterschiedlicher Stärke im Jahreslauf. Einen starken, direkten Einfluss, inklusive antizipatorische Aktivität, hat die nachmittägliche Fütterung. Es kann jedoch nicht mit Bestimmtheit gesagt werden, ob es sich hierbei um einen Zeitgeber oder eine Maskierung handelt.

Die künstliche Beleuchtung in den beiden europäischen Zoos reicht nicht aus, um die Tiere zu entrainen, was in einem unstrukturierten Aktivitätsmuster resultiert. Dies wird besonders im Winter deutlich, wenn der natürliche Tag künstlich verlängert wird. Hier überwiegt der Einfluss der künstlichen Beleuchtung, doch die Aktivitätsmuster verlieren ihre Struktur und zwei der Koalas wurden sogar leicht tagaktiv. Da Koalas nachtaktiv sind, scheint eine Verlängerung des Wintertages unnötig und Tageslängen sollten sich in Zukunft stärker an dem natürlichen Licht orientieren.

Der direkte Kontakt zwischen Pfleger und Koalas, insbesondere das Wiegen, fand während der physiologischen Ruhezeit der Koalas statt. Die Unterbrechung von Ruhezeiten wird als möglicher Stressor angesehen (Wood 1978) und sollte vermieden werden. Pflegerkontakt am Nachmittag wäre demnach akzeptabler für den Koala und resultierte tatsächlich in einer längeren Aktivitäsphase im Zoo Wien. Es ist zudem fraglich, ob tägliches Wiegen als Gesundheitskontrolle notwendig ist, oder ob die regelmäßigen Störungen der Ruhe- und Freßphasen sich nicht eher negativ auswirken.

Häufiger Kontakt mit Besuchern, selbst ohne das sogenannte "Koala-Knuddeln", hat einen deutlichen Einfluß auf das Aktivitätsmuster und das Zeitbudget der Koalas, auch wenn keine direkten Stresssignale gezeigt werden. Daher sollte diese Art von Kontakt minimiert werden. Es ist zudem empfehlenswert, eine systematische Untersuchung von Koalas mit direktem Besucherkontakt unter chronoethologischem Aspekt durchzuführen, um die geltende Rechtslage zum "Koala-Knuddeln" zu überprüfen.

Lebende Baumkronen sind der natürliche Aufenthaltsort für Koalas. Da Koalas in der Wahl ihrer Nahrung sehr wählerisch sind und keiner der Zoos bisher Vergiftungsfälle durch die Nichteukalyptus-Blätter berichtet hat, sollte die Bereitstellung eines lebenden Baumes mit ausreichendem Blattwerk in die Haltungsrichtlinien aufgenommen werden.

Es konnte gezeigt werden, dass ein Anstieg der lokomotorischen Aktivität ein Zeichen für Unwohlsein, Stress oder Östrus sein kann. Hierfür gibt es auch Hinweise in der Literatur (Wood 1978; Zoological Society of San Diego 2001). Weitere Untersuchungen in Kombination mit Hormonmessungen wären sinnvoll, um diesen Parameter zur nichtinvasiven Zustandsmessung zu nutzen.

In dieser Studie konnte der Nutzen der Chronoethologie als Methode zur Überprüfung von Haltungsbedingungen und Gruppendynamik gezeigt werden. Im Unterschied zu traditionelleren ethologischen Methoden ermöglichte sie mir, den Einfluss verschiedener externen Faktoren zu bestimmen und geeignetere Zeiten für den Umgang mit dem Pfleger oder die Fütterung zu finden. Es ist empfehlenswert, daß solche Zoos, die bereits 24-Stunden-Videobeobachtung bei ihren Tieren durchführen, dies unter Berücksichtigung des chronoethologischen Aspektes täten.

The Native Bear, Kur-bo-roo, is the sage counsellor of the Aborigines in all their difficulties. ... The men will seek help from this clumsy creature, but in what way his opinions are made known is nowhere recorded. He is revered if not held sacred.
William Thomas

Chapter 1

Introduction

1.1 Chronobiology and its application in captive management

1.1.1 Circadian rhythms and the internal clock

Life is organised in rhythms. Some of these rhythms are controlled externally, but a variety of rhythms has been proven to be endogenously controlled. The best studied are the circadian rhythms with a period length τ of almost, but not exactly 24 hours. To describe this, Halberg (for review see 1959) introduced the term *circadian*, since the rhythm is circa one day (Latin "dian"). However, endogenous rhythms cover a wide range from one cycle per millisecond on a cellular level to one cycle per several years in an individual or a population (for review see Aschoff 1981b). For rhythms considerably longer than 24 hours, Halberg (1959) introduced the names circalunar and circannual. Also, there is a general discrimination in ultradian ($\tau < 24$ h) and infradian ($\tau > 24$ h) rhythms, especially for those rhythms that do not have an obvious counterpart in the environment (Aschoff *et al.* 1965).

Endogenous rhythms are generated by a system of internal pacemakers ("internal clocks"). We know today that single cells can generate a stable rhythm, but the period length changes, if they are combined to a cell culture or an organ. The best known example for this are the heart muscle cells, where several pacemakers (sinu-atrial node, atrioventricular node, etc.) are able to generate spontaneous rhythms, but are controlled by the fastest pacemaker, the sinu-atrial node (Eckert *et al.* 1993). In mammals the "master clock" that synchronises circadian rhythms of an individual is the Suprachiasmatic Nucleus (SCN) in the lower part of the brain (for review see Klein *et al.* 1991).

Studies have shown that a variety of parameters display endogenous rhythms. The most obvious are the sleep-wake and activity cycles, which show a high stability independent from external stimuli. Other parameters with endogenous periodicity are for example body temperature, hormone concentrations (e.g. melatonin, plasma cortisol) and metabolic rate (for review see Dunlap *et al.* 2003) or visual sensitivity (Fleissner 1974; for review see Fleissner & Fleissner 1998).

There has been much discussion about the use of endogenous rhythms. In a periodic environment, endogenous rhythms make an organism independent from external stimuli and enable it to prepare in time for the predictable, periodic changes of its environment (Dunlap *et al.* 2003). They can be seen as an adaptation to "niches in time" (Aschoff 1964).

1.1.2 Zeitgeber, entrainment and masking

The period length τ of endogenous rhythms is characterised by its rigidity. It is specific for the rhythm and the species, despite some variability among individuals (Dunlap *et al.* 2003). In constant conditions without any changes in light, temperature or any disturbance of the animal, activity, as well as many body functions, will display a stable rhythmicity different from 24 hours. Onset of activity differs for a fixed amount of time between consecutive days; the rhythm is "freerunning".

However, circadian rhythms need to be sensible to external stimuli, for otherwise the organism would fall out of phase with its environment. The synchronisation is done by Zeitgebers, periodic external stimuli of relevance for the organism. They catch a freerunning rhythm and entrain it with the environment (e.g. other individuals, predators, prey). Also, Zeitgebers synchronise the various endogenous rhythms within an organism.

A variety of possible Zeitgebers have been tested, showing that light is the strongest one. Temperature, feeding schedules, social interactions and induced activity can also act as Zeitgeber. One of the characteristics of Zeitgebers is that they not necessarily have a direct effect, but the organism needs a few periods to get entrained to the stimulus. Correspondingly, the Zeitgeber effect does not disappear immediately, if the stimulus is removed. A similar effect can be observed if the stimulus is shifted with a certain angle: the organism follows the Zeitgeber within a few periods (Aschoff 1960).

There are two kinds of Zeitgeber effects. The first is the proportional Zeitgeber, whose effect continues as long as the stimulus is given. The second is the differential Zeitgeber, whose effect depends only on the changing of the factors, while the steady state has no effect. In either case the Zeitgeber needs a certain strength or quality to entrain the organism (Aschoff 1960).

The strength of a Zeitgeber is not absolute, but varies with several factors. Since a Zeitgeber has to be relevant for the organism, there are interspecific differences. Temperature seems to be more effective in exothermic species than in endothermic (Aschoff 1981a). Zeitgeber effects of humidity, air pressure and the electric field have been shown only in few species (for review see Aschoff *et al.* 1982). Even so, individuals of one species react differently to the same Zeitgeber and within one individual, sensitivity changes with life stages, seasons and even daytime (Aschoff 1954). Additionally, the influence of social partners, population size, available space, habitat and weather has been discussed (Aschoff 1954, 1958).

A lack of strength in the Zeitgeber can have different effects. As in constant conditions, the circadian system can start to freerun, until the Zeitgeber stimulus increases in strength. However, not the complete system might be entrained by the Zeitgeber, but only some rhythms, resulting in a "partial entrainment" (Aschoff *et al.* 1982).

In a natural environment several Zeitgebers are experienced by an animal, but usually they are not in conflict with each other and the organism is entrained to the strongest one, usually light (Aschoff 1958). However, in an artificial situation, Zeitgebers might compete with each other. It is possible that some parameters of the circadian system will entrain to another Zeitgeber than the major part of the system. This has been shown for plasma cortisol and urinary cortisone, which can be entrained to periodic feeding in a light:dark regime, while body temperature is entrained by light. It is a case of "selective entrainment" (for review see Aschoff *et al.* 1982).

There are more direct and immediate ways to influence the periodicity of an organism. All known Zeitgebers and a number of other stimuli can act as masking factors that trigger an instant reaction without entraining the organism. Complete darkness for example can inhibit activity, while a short light impulse can result in activity (Aschoff *et al.* 1982). Different to Zeitgebers, the masking effect is only immediate and its lack or shift does not result in a freerun or transient (Aschoff *et al.* 1982). However, in some cases the masking stimulus is transferred through the pacemaker. In this case its strength might vary with circadian time or influence the pacemaker itself as part of a feedback mechanism (Aschoff 1981a; Rietveld *et al.* 1993). Masking is of ecological significance since it enables the organism to react directly and in an appropriate way to a disturbance (Rietveld *et al.* 1993). On the other hand it can represent an inconvenience when it interferes with the activities of the internal oscillator (Rietveld *et al.* 1993).

In a situation with different stimuli affecting an organism, it is not always possible to discriminate between Zeitgeber and masking factor. In case of masking, the reaction comes usually instantly or with a short time lag and ends when the masking factor is removed. There is no anticipation of the stimulus (Rietveld *et al.* 1993). The relation between effect and Zeitgeber is characterised by a phase angle difference. There might be a time lag between Zeitgeber and observed reaction (“delay”) or anticipatory behaviour is observed prior to the Zeitgeber stimulus (“advance”). If the Zeitgeber is shifted, the organism will follow within a few periods, displaying transients (Aschoff 1981a).

1.1.3 Seasonal changes in periodicity

Infradian and circannual rhythms play an important role in reproduction, controlling oestrus, mating or egg deposition (Aschoff 1954), but also in activity. Here it becomes obvious how flexible pacemaker and circadian periodicity can be. Most species are either diurnal or nocturnal, concentrating their activity to a certain part of the day. Often their anatomy and physiology is adapted to these conditions, e.g. special light sensitivity in nocturnal animals (Fleissner & Fleissner 1998). However, during the year, changes in total activity time are smaller than those in day length. Also, the relation between Zeitgeber and onset of activity changes with day length (Aschoff 1969). In daws (*Coloeus mondula* L.) the onset of activity in winter is close to the beginning and end of civil twilight, but in summer close to sunrise and sunset (von Holst 1960 in Aschoff 1969). The end of activity usually varies stronger than the onset. This demonstrates that onset and end of activity are not coupled to a constant Zeitgeber strength throughout the complete year, but sensitivity of the pacemaker changes (for review see Aschoff 1969).

It is possible that not light on/off is important for the phase angle of the organism, but the quality of that change. Aschoff (1969) postulates that twilight is an important stimulus and that the speed of change in light intensity strongly influences the circadian system; the longer the duration of twilight, the earlier the onset of activity and the stronger the sensitivity towards the Zeitgeber. It has been demonstrated that twilight widens the entrainment in hamsters (Boulos *et al.* 2002) and that scorpions are entrained more precisely and with a better internal synchrony by low light intensities (Fleissner & Fleissner 1998).

1.1.4 Animal well-being – a problem of measurement

The well-being of captive animals has become an ethical concern in Western societies. Major requests are adequate housing and the protection from every unnecessary suffering (Scheibe 1997). For zoos, the well-being of their animals is of high priority (WAZA 2005), because next to the ethical considerations it is the basis for longevity and breeding success. A number of methods and criteria for the assessment of well-being have been discussed, but none seems to be satisfactory on its own. The discussion begins with a valid definition of well-being and the question which criteria have to be considered (Dawkins 1976; Broom 1991; Fraser 1993; Scheibe 1997).

A generally accepted assessment of well-being is the measuring of "stress" as defined by Selye (1950), who focussed on the increased activity of the hypothalamic-pituitary-adrenal axis. However, a reduction of well-being to a small group of hormones seems to be an inadequate method. Dietrich von Holst (1998, p. 6) warns that

> "Although, even by today's standards, this approach may appear attractive methodologically, it is important not to equate stress with adrenocortical function, as the responses of an organism to new and sudden demands comprise almost all physiological systems. Heightened adrenocortical activity constitutes only one part of this response pattern and is in no way sufficient to characterize the stress state of an animal, especially because adaptive responses to stressful situations may occur without any heightened adrenocortical activity."

Moberg (2000), too, advises against the uncritical use of hormone levels, referring to a study of Colborn et al. (1991), in which stallions secreted the same amount of cortisol whether they were restrained, exercised or permitted to mate with a mare. Wingfield et al. (1998) states that under long-term stress animals enter an "emergency life history stage", in which behaviour and physiology are changed, but glucocorticosteroids are not always increased. They postulate that this enables the organism to deal with the stressor without suffering the consequences of physiological stress, including immune suppression, inhibition of growth and total failure of reproductive function. Broom (1988), too, argues that animals living under difficult conditions for a long time might have adopted strategies to deal with the situation. Often these strategies involve changes in behaviour.

In a review, Fraser (1993) gives a number of arguments against Selye's stress theory. He argues that classical stressors as defined by Selye do not affect only the adrenal cortex, but all major endocrine systems and an increase in glucocorticoid activity is not restricted to unpleasant situations. He also stresses the methodical problems: for once, the experimental situation itself might be stressful for the animal; secondly, the pulsatile secretion of cortisol has a strong influence on plasma concentration.

Also, glucocorticoid measurements have given disappointing results. Tammar wallabies (*Macropus eugenii*) did not show significant variations in plasma cortisol levels during periods of disturbance, but in faecal cortisol levels (McKenzie & Deane 2005). In restricted bulls, ACTH and cortisol responses were greatly reduced after three days, but for the remaining 46 days of restriction, behaviour was aberrant (Munksgaard *et al.* 1999). This reduction of adrenal medullary activity makes stress hormones inadequate for the long-term measurement of well-being (Broom 1988).

Furthermore, well-being is not only defined by stress. An organism can experience a variety of inconveniences, restrictions, pain or diseases that influence its well-being. Dawkins (1976) emphasises the fact that we do not know what an animal feels and the need to be careful not to transfer human criteria on them. Therefore, she asks for new methods to assess well-being in animals. Broom (1988) warns, that if one indicator does not show problems in well-being, another one might. So, he advises to combine several methods for an adequate evaluation. He (1988, p. 17) also advises that

> "Any recognition of good welfare should be carried out at various times during the animals' daily routine and should be combined with the use of indicators of poor welfare, because an individual's welfare might be good at one time during its life in given conditions but poor at other times."

1.1.5 Chronoethology – a tool to measure animal well-being?

Several authors suggest the use of behaviour as an indicator for well-being (Dawkins 1976; Broom 1988; Fraser 1993; Cook *et al.* 2000). Rushen (2000, p.37) states that

> "The attractiveness of behavioural indices of stress lies in the fact that they are quicker and appear technically easier to obtain than physiological measure. In addition, they are considered to reflect more directly the animal's feelings or emotions."

A decrease in well-being in many animals involves changes in behaviour (for review see Broom 1988). Stereotypies have been shown to decrease physiological stress symptoms and are now generally accepted as coping strategy. Other animals might react with apathy. So far, no obvious stereotypies have been observed in koalas (e.g. Smith 1979a)

The temporal pattern of behaviour, though rigid in its endogenous periodicity, is influenced by a variety of external and internal factors. In captivity, Zeitgebers often differ in their quality from the natural situations. Artificial light regimes in indoor enclosure might lack the quality to entrain an organism and lead to a decrease in well-being (Seidel *et al.* 1999). Feeding times and handling influence the periodicity either via the pacemaker or directly as masking factor . Furthermore group composition can play a role, especially if it is not similar to the natural situation (Aschoff *et al.* 1982). Therefore, the housing conditions of an animal should be reflected in its behavioural periodicity and activity pattern.

On the other hand, the internal state of an animal influences its rhythmicity too. As described in 1.1.2 and 1.1.3 the sensitivity of an animal towards a Zeitgeber varies with its life stage. Many factors are known to have a direct influence on activity, including pain, disease, interruption of a necessary behaviour (e.g. feeding, resting) and behavioural deprivation. Some of them might result in clinical symptoms, but if this is not the case, the animal might still suffer and it is necessary to recognise such suffering (Dawkins 1988). Several studies have shown that a chronoethological observation helps to detect aberrations from a normal behaviour pattern at an early stage and therefore give information on the internal state of an animal and in many cases the factors influencing it (Sebisch *et al.* 1997; Scheibe *et al.* 1999; Seidel *et al.* 1999; Berger *et al.* 2003; Fleissner 2003; Benesch *et al.* 2005a; Benesch *et al.* 2005b; Schubert 2006).

1.2 The Koala, *Phascolarctos cinereus*, Goldfuss 1817

Next to the kangaroo, the koala is probably Australia's best known animal and its most charming icon. It can be found in most zoos and wildlife parks in Australia and to hold a koala or at least to get a photo standing next to one is on the top of the list of most tourists. Often referred to as a "cuddly teddy bear", the koala holds many surprises in its pouch.

1.2.1 Taxonomy and anatomy

Taxonomy after Strahan 1995

Subclass	Marsupialia
Order	Diprodonta
Suborder	Vombatiformes
Superfamily	Phalangeroidea
Family	Phascolarctidae
	Phascolarctos cinereus (3 subspecies):
	P. c. cinereus, Goldfuss 1817, in New South Wales
	P. c. adustus, Oldfield Thomas (1923), in Queensland
	P. c. victor, Ellis Troughton (1935), in Victoria

The koala is the only species in the family Phascolarctidae. Its taxonomy was subject to much speculation. Early explorers referred to the koala as monkey or marsupial bear. The latter has survived until today in English as well as in German ("koala bear" or German

Figure 1.1: a: Female koala resting in tree. Koalas display a variety of resting positions. This position is preferred on warm, dry days. b: Male koala running on ground (Photo by Ingo Weidig). Males are bigger than females. When running on ground, koalas galop, moving first both front, than both hindlimbs.

"Koalabär"). Nevertheless, the koala has nothing in common with bears, except for some similarity in appearance.

Koalas are strictly herbivorous and belong to the same order as possums, wallabies and kangaroos (Strahan 1995). Originally, it was placed within the family Phalangeridae (brushtail possums, cuscuses, scaly-tailed possums) due to its arboreal lifestyle and similarities in the anatomy of the hands (see below) (Thomas 1888; Bensley 1903; Lee & Martin 1988), but modern research has shown that the closest relative of the koala is the wombat (*Lasiorhinus krefftii*, *L. latifrons* and *Vombatus ursinus*, Vombatidae) (Lee & Martin 1988). This might be surprising since the wombat, as a burrowing marsupial, lives on and underneath the ground, but analysis of the sperm and blood serum supported the relationship (Lee & Martin 1988). Other similarities between the koala and wombat are the rudimentary tail and the backwards opening pouch. In possums and macropods, the pouch opens front- or upwards to prevent the joey (pouch young) from falling out while the mother climbs or jumps. This prevents soil from entering the pouch during burrowing, a behaviour not seen in the koala (Lee & Martin 1988).

The koala is rather short and stout with relatively long extremities (Fig.1.1). Its muscular body is covered with a soft, dense fur that protects the koala from rain and cold. It is one of the best insulating mammalian furs outside the polar areas (Cronin 1987). The fur on the back is grey with whitish specks around the bottom, while the breast and belly are white. In males, a gland secreting a red fluid is situated in the centre of the breast. The tail is not visible.

The head is relatively big, in males it is broader and squarer than in females (Lee & Martin 1988). The eyes with the vertically slit pupil are rather small and positioned forward. Since they are mainly nocturnal, koalas have a *tapetum lucidum*, a layer that reflects the light back through the retina. The small ears sit on top of the head. The whole ear, including the opening, is covered with fur. The protruding nose is big and covered with soft, usually black, leathery skin. The rhinarium (wet area around the nostrils) is well developed and almost reaches up to the eyes (Lee & Martin 1988).

The hands are similar to that of many arboreal possums (Lee & Martin 1988) (Fig.1.2). Thumb and index finger oppose the other fingers. This forcipate hand enables the koala to get a good grip on the branches. All fingers have long, sharp claws. The feet are different from other arboreal marsupials. The hallux (big toe) sticks out at right angles to the main line of the foot and is rather stout but lacks a claw. The fourth and fifth toes build the antagonists, while the second and third toes are fused together by skin to serve as a comb. Hands and feet have only a weakly granulated surface, as in most arboreal mammals (Lee & Martin 1988).

Based on differences in size, fur and habitat, three subspecies have been postulated: *P. c. adustus* from Queensland, *P. c. cinereus* from New South Wales and *P. c. victor* from Victoria (Strahan 1995). Koalas from Victoria are bigger in size and have a denser, longer and darker fur than the ones from further north, but these differences as well as genetic variations are not consistent with state borders and can be explained as normal intraspecific variations due to the climate (Houlden et al. 1999; Sherwin et al. 2000; Thompson 2002). Today, the classification into subspecies is not commonly accepted (Lee & Martin

Figure 1.2: a: Koala hand. Note the "double thumb" and the long claws. b: Koala foot. The big toe lacks a claw, the second and third toe are fused together by skin to serve as a comb.

1988; Takami *et al.* 1998).

Little is known about the evolution of the koala, but it seems that koalas have not changed much during the last 25 Mio. years (Archer et al. 1994). So far, twelve extinct species from four genera are known, some of which have been sympatric. All of them were arboreal and folivorous, but over time, the habitat alternated between open forest and rainforest (Lee & Martin 1988). Size differed between 66 and 130% of the modern koala. Today's size seems to be ideal for a mammal especially adapted to eucalyptus.

1.2.2 Habitat, distribution and status

Koalas are arboreal. They are only seldom seen on the ground. They might venture onto the ground when they change trees or, especially in the case of young males, when they search for new territory. Today, koalas can be found only along the East Coast and Eastern South Coast of Australia where they inhabit open eucalyptus forests (Fig. 1.3). Koalas are relatively tolerant to climate and can be found in the cold temperate areas of Victoria as well as in the tropical forests in Queensland (Moeller & Grzimek 1988).

Not all eucalyptus forest is inhabited by koalas. They prefer coastal and open forest or areas close to water, but avoid wet forests or southern areas higher than 600 m (Lee & Martin 1988). The actual number of koalas in an area depends on tree species, tree density, rainfall, climate and soil (Sharp 1995). In addition to food trees, koalas use non-eucalyptus

Figure 1.3: Natural distribution area of the koala *Phascolarctos cinereus*. Modified from Australian Koala Foundation, 2006.

trees for resting (Sharpe 1980).

The status of the koala is not completely clear. The IUCN Red List classified the koala as “Low risk near threatened” in 1996 (Australasian Marsupial & Monotreme Specialist Group 2006) and it is not listed in the appendices of CITES (CITES 2006). In Australia the official status varies with state: it is listed as “rare” in South Australia, “vulnerable” in New South Wales and in the South East Queensland bioregion and “common” in the remaining Queensland. It is not listed in Victoria (Australian Koala Foundation 2006, 18.09.2006). Western Australia, Tasmania and the Northern Territory do not have any wild koala populations.

Population size differs greatly between studies, ranging from 45 000 - 80 000 koalas in all of Australia (estimated by the Australian Koala Foundation in 1995 (Sharp 1995)), to one million koalas for Victoria (Phillips 2000). In 1986, the Australian National Parks and Wildlife Service estimated that there were 400 000 koalas in the whole of Australia (Sharp 1995; Thompson 2002). A clear estimate seems to be particularly difficult since population density varies with several habitat parameters and differs strongly between geographical areas. While there have been local extinctions in New South Wales since 1970 (Lunney et al. 1993), overabundances are known from places like Kangaroo Island (South Australia), where the population was estimated to contain $\sim$ 27 000 koalas in 2001 (Masters et al. 2004). Some researchers even argue that population numbers of koalas have always been low and that recent numbers are higher than those during other paleontologically known periods (Archer *et al.* 1994).

But although there is no generally accepted number of koalas, it has been commonly agreed that the koala population needs to be stabilised to keep one of the most adored and economically valuable icons of Australia healthy. Recent koala populations are isolated from each other. In the 1990s, 80% of the koalas lived on private land, which is suitable for farming and urban development (Sharp 1995). There also has been a noticeable decline of koalas in various areas (Phillips 2000). The National Koala Network (Australian and New Zealand Environment and Conservation Council 1998) has therefore campaigned for an increase in the protection of koala habitats, the development of a better understanding of the biology of the koala, ready access to information about koalas for the public, and higher standards in husbandry for captive, sick or injured wild koalas.

1.2.3 Nutrition and digestion

Koalas have a special diet of eucalyptus leaves. There are about 750 different species of eucalyptus in Australia, but only about 30 have been reported as being consumed by koalas (Lee & Martin 1988; Sharp 1995). The actual number of food species varies between individuals, habitat and season.

In addition to the koala, only three other species are known to feed on eucalyptus leaves: the brushtail possum (*Trichosurus vulpecula*), the common ringtail possum (*Pseudocheirus peregrinus*) and the greater glider (*Petauroides volans*). To all other mammals eucalyptus is toxic (Cronin 1987; Lee & Martin 1988; Sharp 1995). Humans use eucalyptus because of its strong smell and disinfecting properties.

Koalas eat between 200 and 1250 g of leaves per day (Lee & Martin 1988; Moeller & Grzimek 1988). The leaves are rich in water (40-60%), and therefore koalas only need to drink on very hot days. However, the leaves are low in protein and fat. In addition, eucalyptus is high in toxic substances, especially tannin, phenol, cineol and phellandren (Cronin 1987; Lee & Martin 1988). Every day koalas consume a dose of these substances lethal for a human. The toxins are usually broken down in the liver, which is of a deep violet colour. If toxin concentrations become too high, the koalas can slowly die (Cronin 1987; Martin & Handasyde 1995).

Due to the toxicity of the leaves, koalas carefully choose leaves by sniffing (Fig. 1.4a). Usually the young tips are preferred. Several studies have focussed on the decisive factors for the choice of a leaf, but the results are different and sometimes contradictory (Betts 1978; Southwell 1978; Ullrey *et al.* 1981a; Zoidis & Markowitz 1992; Hume & Esson 1993). Since eucalyptus is very rich in fibre, a high consumption of leaves is not possible because it swells in the gut and prevents further food intake (Cronin 1987). To increase the efficiency of food intake, the digestive system shows some special adaptations. The molars have sharp crests and strong enamel, so leaves are chewed thoroughly (Cronin 1987). Harrop and Degabriele (1976) report that the koala has the longest caecum (in relative terms) known in mammals. Gut content is separated before entering the caecum into small, digestible particles and fibre (Cronin 1987). While fibre is excreted after 24-48 hours (Cronin 1987), Cork and Warner (1983) found gut passages lasting up to 213 hours for the particles in the caecum. The bacterial flora of the caecum is of importance; its composition changes with season, body conditions and systematic antibiotic therapy (Lee & Carrick 1989). In stressful situations, dead koalas have been found with a filled gut; it is possible that the separation mechanism does not work properly when a koala is under stress (Cronin 1987).

Since eucalyptus is low in calcium, koalas have been observed eating soil (Cronin 1987). In several cases, koalas have been seen to feed on non-eucalyptus plants like native kapok (*Bombax malaberica*), *Acacia costata,* the north-American Monterey Pine (*Pinus radiata*) and apple (*Malus communis*) (Cronin 1987; Lee & Martin 1988; Sharp 1995). In cap-

Figure 1.4: a: Joung koala is sniffing on eucalypt leaves. The young tips are preferred food. b: Female and male koala at Taronga Zoo. Though koalas are solitary, they can be kept together in captivity. However, close encounters might be tense or aggressive.

tivity, koalas sometimes also take fruit, sandwiches, cookies and ice-cream (Cooper *pers. comm.*; *pers. obs.*). So far, it is not known if koalas can digest other plants or if they are able to survive without eucalyptus (Lee & Martin 1988).

To avoid poisoning through too much eucalyptus intake, koalas also have some adaptations to save energy. The most obvious is the low activity observed in koalas (see 1.2.5). The metabolic rate of the koala is only 70% of that predicted for a marsupial of its size (Degabriele & Dawson 1979). Its daily energy requirements have been calculated as 2090 KJ, an equivalent to 510 g leaves. Furthermore the brain is one of the smallest in mammals, with only 60% of the volume predicted for a mammal of that size (Lee & Martin 1988).

1.2.4 Social structure

Koalas are considered to be territorial. Eberhard (1978) found that a territory consists of 14 – 15 trees, but this depends strongly on the tree species, the climate and the general character of the area (Sharp 1995). The home range of female koalas on Kangaroo Island varied between seven and 176 m^2, while that of male koalas ranged between 80 and 176 m^2. Nevertheless, some individuals rarely changed trees (Cronin 1987). Males move more often and for longer distances than females and therefore experience more encounters with other koalas (Mitchell 1990).

Koalas are solitary and are usually found on their own or, in case of females, with their dependent cub (Lee & Martin 1988; Martin & Handasyde 1995). Although some trees were used by more than one koala, only in a few cases have two adult koalas been observed in one tree at the same time (Cronin 1987). However, in the last years evidence for a social system is increasing. Sharp (1995) reports a complex social, hierarchical structure in which an α-male with a bigger home range dominates the males in the surrounding area. If these key-individuals are removed from a population, the social organization of the remaining animals loses stability (Sharp 1995). A male's home range overlaps with the home ranges of several females, whose home ranges are smaller (Sharp 1995).

Due to the solitary lifestyle of koalas, little social behaviour has been observed, usually only between mother and cub (Smith 1979b). Communication is mainly vocal, with a variety of sounds being used; these have been studied extensively by Smith (Smith 1979b, 1980a). The most obvious is the bellowing, a series of deep snoring sounds. Bellowing is primarily observed in males and shows a clear seasonal variation: bellowing peaks during the breeding season. Males often bellow if another male approaches, prior to or after a fight, but also without any recognizable external stimulus. Females also bellow sometimes, but this is a shorter sound with less intensity than in males and more strongly related to external stimuli like a fight with another female (Smith 1980a). Additionally, koalas use a variety of squeaks, squawks, grunts, snarls, wails and screams, especially in aggressive or stressful situations. Facial expressions are rare (Smith 1980a) (Fig. 1.4b), but flicking of the ears is well known as a sign of discomfort (Thompson 1987; Kindemi *pers. comm.*; Tobley *pers. comm.*). This ear flicking is sometimes seen in nursing mothers when the pouch young becomes overzealous in its sucking attempts.

1.2.5 Chronobiology and time budget

So far, no systematic study on the chronoethology of koalas exists. In general, the koala is considered to be nocturnal, but several studies in the last 40 years have shown that, although most activity occurs during the night and especially twilight, there is also some activity during daytime.

Robbins and Russell (1978) studied four males in a semi-natural situation. They found an apparent peak in feeding in the evening from 16:00 to 20:00 and only little feeding in the morning between 11:00 and 14:00. Feeding was related to sunset and 66% of feeding was observed during the night. Locomotion did not differ between day and night.

Nagy and Martin observed four female koalas for 24 hours in their natural habitat using binoculars. They found no clear cut restriction of activity to day or night, although feeding activity was more frequent just before sunset (16:00 – 19:00) and in mid-morning (08:00 – 10:00). The koalas spent on average 4.7 h eating, 4 min travelling, 4.8 h resting while awake, and 14.5 h sleeping. The activity patterns showed strong individual variations. Body temperature rose slightly when the animal was active and fell during sleep, but no clear circadian pattern was found.

Mitchell (1990) observed feeding, moving and social behaviour in free ranging koalas more often during the night (77% of all feeding observations). During the breeding season, males changed trees in between days more often, also the distances between locations were greater for males. Older males moved more often and for longer distances than young ones. Especially during the breeding season, the home ranges of males were bigger than those of females. Females did not avoid the home ranges of other koalas, but encounters with mates were mostly initiated by the males.

Pieters and Woodall (1990) studied the daily movement patterns of free-ranging koalas in Queensland and found a considerable variability in average daily movements. The females in this study covered on average less than half the distance of the males and used fewer trees, though their home range did not differ. 86% of the koalas were found in the same tree in the morning as in the evening before. The time spent in one tree seemed to depend on food quality; koalas stayed longer at high quality food sources.

So far there is only one systematic study on koalas in zoological gardens, which was conducted at Lone Pine Sanctuary, Brisbane (Smith 1979a,b, 1980a,b,c). It includes social behaviour and vocalization. Unfortunately observations took place only during daytime. Smith (1979a) found a strong influence of the keeper: After fresh leaves had been introduced by the keeper in mid-afternoon, nearly all animals fed for about an hour and afterwards irregularly throughout the rest of the day.

1.2.6 Reproductive biology

Koalas are polyoestrous seasonal breeders. The oestrus has a thirty-day cycle and takes place between September and March (southern spring and summer) (Lee & Martin 1988; Sharp 1995). Oestrus is often characterised by prolonged periods of activity in females (Smith 1980c). The literature is divided as to whether the male or the female initiates mating (Cronin 1987; Sharp 1995).

In zoological gardens, specific oestrus behaviours have been observed in females. Smith (1980c) describes what he calls "jerking": "The female clings vertically to a tree and her whole body, or less often the upper part alone, jerks upwards vigorously about once a second. At the same time the head jerks backwards and the ears are flicked, independently of the general body movements." He also observed bellowing, which is usually performed by males in connection with fighting. Some females showed aggressions towards males and in a milder form towards females as well as pseudomale behaviour like mounting another female. Thompson (2002) additionally reports an increase in activity and weight loss in the San Diego Zoo population. But usually, oestrus behaviour is rare and brief due to the short duration of oestrus and the fast reaction of males in the area (Smith 1980c). Smith (1980c) describes a total lack of male courtship. The female in oestrus is usually ready to react, but it might take some time before she actually permits copulation. During copulation, the female tries to free herself from the male by struggling, biting and screaming (Smith 1980c; Lee & Martin 1988). Copulation lasts on average only 1.5 minutes and is the shortest known in marsupials (Smith 1980c). In captivity, males have been observed to attempt mating with non-oestrus females, but without success (Cronin 1987). The actual oestrus lasts several hours in captivity and probably one to two days in the wild.

The pouch of the koala is tightly closed by a sphincter muscle. After only 35 days of gestation, a koala is born naked, blind, with clawed arms and rudimentary developed legs (Lee & Martin 1988; Sharp 1995). Measuring only 19 mm and about 1 g, which is $^{17}/_{1000}$ of the mother's weight, it is similar to the embryo of a placental mammal (Cronin 1987; Sharp 1995). Koalas have a well developed placenta, which connects mother and embryo during the first month of gestation (Strahan 1995). During the birth, the mother leans backwards with hips thrust out and legs wide open. The young climbs up to the pouch using its strong clawed arms, where it attaches itself to one of the teats. On its way, it leaves a small line of slime, which can be used to detect birth (Thompson 1987, 2002). While the young koala, the so-called joey, is in the pouch, there seems to be no mother-child interaction, not even cleaning of the pouch (Lee & Martin 1988). After 21 weeks the eyes open and the young koala sometimes peeks out of the pouch (Sharp 1995). Now it starts to feed on "pap", a special faeces containing gut bacteria and vitamins (Sharp 1995). After 23 weeks the joey has its complete coat of fur and the first teeth emerge (Lee & Martin 1988). After 25 weeks, the joey weighs 250 g and starts to leave the pouch (Lee & Martin 1988).

The mother sometimes licks the joey (Lee & Martin 1988) and in several cases, behavioural interplay has been observed: the joey climbs over the mother, which tolerates it, but rarely actively plays (Cronin 1987; Sharp 1995). It will return to the pouch until at least week 28, when it has grown too big and stays on the mother's back or in her lap (Cronin 1987). In its tenth month, the joey will leave its mother for short excursions, but it will be another two months until it is weaned and becomes independent (Martin & Handasyde 1995; Sharp 1995). If a joey loses its mother, it calls for her. This call is answered by all adult koalas in reach (Cronin 1987). Joeys do not necessarily recognize their mother and will climb on the back of every available adult koala (Cronin 1987; Lee & Martin 1988). Koalas can give birth to one joey per year, but often the period between joeys is two years (Lee & Martin 1988; Martin & Handasyde 1995).

1.2.7 Koalas in captivity

The koala is perhaps the most appealing Australian animal. Many tourists hope to see a koala in the wild or at least in a zoo (Hundloe & Hamilton 1997). For those who are not able to travel to Australia, zoos in their home country are an opportunity to see the charismatic Australian. Nevertheless, koalas are rare in European zoos, for they are to the present day considered to be a problematic species (Schratter *pers. comm.*; Winkler *pers. comm.*).

1.2.7.1 History

The history of koalas in zoos is full of disappointment, hope and emotion. On 28 April 1880, the first "marsupial bear" arrived in London. He had survived the long journey on fresh and dried leaves but unfortunately died 14 months later at London Zoo in an accident. The next koalas to come to Europe died during the journey. In 1920, the zoo of New York attempted to show a koala, but the animal died after five days. In the same year, the first Australian zoo, Koala Park in Pennant Hill, Sydney showed koalas to its visitors (Grzimek 1979/80).

To keep koalas in overseas zoos turned out to be difficult, but one zoo did not give up: San Diego Zoo, USA, received its first pair of koalas on 28 January 1925, but they died within the next two years. 1928 a second female arrived, but survived for only seven months. 1952 two breeding pairs arrived from Australia. This time they survived six years. In the next year, 1959, one male and two female koalas arrived from Taronga Zoo. One of these females already had a pouch young (Crandall 1964). A second one was born 1960. Between 1959 and 1979, 14 koalas were born at San Diego Zoo. To refresh the population, two male and four female koalas arrived from Lone Pine Sanctuary in Brisbane. In cooperation with Lone Pine, the husbandry guidelines were completely changed. More koalas followed from Lone Pine and in 1987, San Diego owned the biggest koala population outside of Australia. The first koalas left San Diego Zoo in 1988 for loan to other North-American zoos. In 1989, the first San Diego koalas crossed the ocean to Europe (Thompson 1987, 2002). Until 2002, San Diego had 70 koalas in loan to 54 cities and 11 countries (Doyle et al. 2002).

In 1994, two males were sent from San Diego Zoo to Duisburg Zoo, Germany. A female followed and in 1995 the first "European" koala was born (Thompson 2002). Ever since, Duisburg Zoo has been breeding successfully. Today, eight European zoos keep a total of 24 koalas (ISIS 2006). These koalas are exclusively loans from San Diego Zoo and are kept under strict supervision to ensure high management standards (Zoological Society of San Diego 2001; Schratter *pers. comm.*)

While San Diego was breeding koalas for North America, Japan started its own koala husbandry program. In 1983, Taronga Zoo prepared a group of koalas for Tama Zoo (Tokyo) and Higashiyama Zoo (Nagoya). Keepers and veterinarians were brought to Australia to be trained in koala management. Emotions were strong during this cooperation: When the koalas were finally ready to leave their home zoo, everybody was so excited that David Butcher, the Sydney veterinarian, who accompanied the koalas, forgot to pack personal items into his suitcase. The koalas' well-being was simply more important. In the following years, the koalas thrived and bred in Japan. More zoos followed and today, there are more than 100 koalas in Japanese zoos (Clements 2002).

1.2.7.2 Problems

Although breeding success in zoos is common, koalas are considered to be a problematic zoo species due to a variety of reasons. The biggest issue in koala husbandry is the food. Since koalas are very selective, they have to be fed a variety of eucalyptus species and need a larger amount of leaves than is actually consumed to enable the koalas to choose their leaves (Sharp 1995). Also, leaves have to be fresh. This is especially problematic for overseas zoos in cold climate areas, since most food species are not frost-resistant. At Duisburg Zoo, eucalyptus branches are flown in from Florida twice a week at high costs (Kindemi *pers. comm.*). But even Australian zoos have problems maintaining an adequate and sufficiently varied food supply throughout the year. The eucalyptus species growing in the area around the zoo might not be the species accepted by the koalas or might not grow in the necessary amount. In addition, food quality varies between seasons. Some zoos started programs with neighbours and schools to grow koala food trees (Carrick et al. 1990; Gifford *pers. comm.*).

A much more complex problem is the well-being of koalas. Koalas suffer from a variety of diseases, of which the most common and often lethal one is chlamydiosis (Cronin 1987; Martin & Handasyde 1995; Sharp 1995). This infection with *Chlamydia psittaci*, the psittacosis-agent, is transmitted sexually and affects the urogenital tract (resulting in the „wet bottom" or „dirty tail" syndrome), the eyes and the respiratory tract. It seems that stressed animals are more prone to chlamydiosis (Cronin 1987).

In general, stress is considered to be the most common cause of death of captive koalas in Australia (Wood 1978). Stress in koalas can be caused by handling, especially by unfamiliar and untrained keepers, disruption of feeding and sleeping times, overcrowding relative to the wild state, separation of sexes, controlled mating and controlled weaning (Wood 1978; Thompson 1987). Nevertheless, hand-raised koalas grow accustomed to handling quite easily and like to be carried around (Grzimek 1979/80; Cronin 1987). In some zoos, koalas are kept in crowded conditions without showing obvious signs of stress and aggression (Cronin 1987), but Sharp (Sharp 1995) mentions territorial behaviour in males held under such conditions.

Immediate stress responses are vocalisations (“stress hum”), hiccupping, ear twitching or stiff body posture with eyes wide open and ears held up (Zoological Society of San Diego 2001; Yusuf & Rosenthal *unpublished data*). Presence on the ground is usually a sign that something is wrong. This includes inadequate enclosures (e.g. too few resting forks), low food-quality, disease, the presence of stressors in the environment, excessive handling or mishandling, temperature extremes and overcrowding of koalas. It might also indicate oestrus in females, or breeding restlessness in males if in proximity of an oestrus female (Zoological Society of San Diego 2001).

Long-term symptoms include change of weight and loss of fur (Carrick *et al.* 1990; Gordon 1990), but these symptoms might also be caused by other factors like diseases. Carrick and Wood (1990) tested an empirical "Condition Index Score” based on the development of muscle mass, but found body weight to be a very ineffective index of well-being in koalas. Nevertheless, San Diego Zoo recommends daily weighing of koalas to monitor health conditions (Zoological Society of San Diego 2001). But due to handling and interruption of resting such weighing might be a stressor itself (Wood 1978; Zoological Society of San Diego 2001).

Wood (1978) also mentions the so-called Wasting Disease, a progressive wasting condition resulting in death. It can be diagnosed by palpation and cured if diagnosed early. In wild koalas, Obendorf (1983) describes the “koala stress syndrome”. It is characterised by “lassitude, depression, anorexia and a precipitous decline in metabolic functions”. Koalas were found wandering on the ground aimlessly or comatose without evidence of trauma or illness. This disease usually results in death, and the autopsy shows signs of dehydration, loss of muscle bulk, atrophy of lymphoid follicles in spleen and lymph nodes and a decrease of size and number in adrenal cortical cells. There have also been occasions of koalas dying with a filled gut, which is thought to be due to a stress-induced failure of the digestive system (Cronin 1987). Unfortunately, some of these signs cannot be used to assess long-term stress. Also, health in koalas can deteriorate beyond recovery at an alarming rate without the koala showing obvious signs of ill health or stress (Zoological Society of San Diego 2001). Therefore, evaluation of the status of the koala needs training of the keeper which is not provided in all Australian zoos (Carrick *et al.* 1990; Douglas 1990). It is also necessary to find additional methods to monitor and validate koala well-being.

1.2.7.3 Koala and visitors

The koala has become a marketing symbol for Australia. In a survey by the Australia Institute, 75% of overseas visitors said they wanted to see a koala on their holiday. This made it the most sought-after Australian animal (Hundloe & Hamilton 1997). Cuddling a koala is a highlight for overseas tourists, especially for the Japanese (Fujiki 1997). Several wildlife parks in Queensland sell photos of visitors "cuddling" a koala. Up to 85% of these pictures in 1996 were sold to overseas tourists. Including koala merchandise and travelling costs for seeing koalas, the Australia Institute estimates that in 1996, between A$ 336 million and A$ 1.8 billion have been spent on koala tourism (Hundloe & Hamilton 1997). So, aside from its ecological value, the koala has a significant economic value for Australia.

In the 1990s, an Australian wide discussion was started on the question if hugging and handling by visitors is stressful for the koalas or if they like to be "cuddled". This discussion has often been emotional on one side and ruled by commercial reasons on the other (see debate of NSW Legislative Council Hansard, 21 November 1995 (NSW Legislative Council Hansard 1995)). In 1995, the government of New South Wales passed an act of legislation banning the holding and cuddling of koalas by visitors from 1997 (Exhibited Animals Protection Act, NSW, 1997). However, the Inbound Tourist Organisation of Australia (ITOA) argued that the state of New South Wales would lose A$ 60 million annually, because tourists would choose to go to Queensland instead, where "koala hugging" was still allowed. Here, zoo koalas are kept on a strict handling schedule. In Lone Pine Sanctuary in Brisbane, Queensland, koalas are not allowed to be handled for more than 30 minutes and three days in a row to avoid health problems (Lone Pine Sanctuary 2006).

Cronin (1987) and Wood (1978) mention handling and constant attention as a reason for indisposition or stress. San Diego Zoo recommends handling only by experienced keepers known to the koalas and does not permit VIPs or photographers inside the enclosures (Zoological Society of San Diego 2001). But so far, no systematic research has been done on “koala-cuddling”. It seems that such studies are generally missing for zoo animals (Kreger & Mench 1995). However, it is known from primates that the simple presence of visitors in front of zoo exhibits can result in disruptions and aberrations of behaviour (Kreger & Mench 1995).

So far, a systematic research on handling by visitors is lacking and discussions have been based on personal experience and opinions. In June 2003, a pilot study was conducted by two students at the Koala Encounter, Taronga Zoo to assess the potential impact on no-contact photo-sessions with visitors on the koalas (Hoetelmans & Kregten 2003). Direct observation during the photo-sessions was used and behaviour with and without visitors was compared. The results included some possible signs of stress, like increased alertness, interactions and ear twitching, but it was not clear if these were related to stress or to other factors. Also, the length of observation was too short. Therefore, it is necessary to obtain more detailed data on this topic.

1.3 Aims of this study

As has been implied by several authors (Dawkins 1976; Moberg 1985; Broom 1988; Yousef 1988; Broom 1991; Fraser 1993; von Holst 1998), there still is a want for simple and effective methods to assess animal well-being, preferably in a non-invasive way. Chronoethology analyses the pattern of activity and behaviour. Zeitgeber quality, masking or interruptions are reflected in these patterns (Fleissner 2003), and they can be used to evaluate the conditions and their implementation on the well-being of the organism (Berger *et al.* 2003). Koalas are in need of such a method, since health issues are common in captive koalas (Wood 1978; Carrick *et al.* 1990; Douglas 1990). With traditional assessments, problems may not be recognised early enough, or the evaluation process itself, e.g. weighing, might reduce well-being in the koala (Wood 1978). Therefore, the present study focuses on activity pattern in captive koalas and the exogenous influences on them.

- Koalas under natural light and climate conditions in an Australian zoo are observed for one year to obtain norm-actograms under changing seasonal conditions

- Those norm-actograms will be compared to actograms of koalas in indoor enclosures of Duisburg and Vienna Zoo, Europe

- The influence of light, keeper activity food presentation and handling will be tested on Zeitgeber properties. Appropriate time for handling will be tested.

- Actograms of koalas with moderate visitor contact will be compared with the norm-actograms for possible signs of low well-being

Four housing conditions in three different zoos have been compared:

Sydney (Taronga Zoo), Australia

- within the natural distribution area of koalas: light regime and climate are natural for free-ranging koalas
- outdoor enclosure: natural light regime and changing weather

Koala Walkabout

- breeding group with one male and two to four females including joeys, number of females changes due to breeding plan
- hands-off management, koalas are irregularly handled, not more often than once a month
- fixed feeding time at 15:30 combined with about 15 minutes Keeper's Talk

Koala Encounter

- two small groups of two adult females, in one case with a 12 months old female joey
- visitors allowed in enclosure for two hours per day, no direct contact allowed
- hands-on management by the keepers, koalas are usually weighed every second week
- three fixed feeding times at 07:00, 11:00 and 13:00

Duisburg Zoo, Germany

- Northern hemisphere, seasons shifted by 6 months
- indoor enclosure with artificial light regime; artificial day length constant plus damped natural light through frosted-glass sky-lights
- one male, separated from group of three females with one joey

- moderate hands-on management, koalas are weighed twice a week, frequent contact during long morning cleaning session
- feeding at different times during the morning

Vienna Zoo (Tierpark Schönbrunn), Austria

- Northern hemisphere, seasons shifted by 6 months
- indoor enclosure with artificial light regime; artificial day length constant plus natural light through large sky-lights
- one male and one female kept separately
- hands-on management, koalas are weighed daily, especially the female is carried around and taken out of the enclosure by the keeper regularly
- two feeding times per day, one during morning cleaning, and a second one after the weighing at 10:15

...if you...go home every day at 5 o'clock,
you might be missing something.
ADRIAN HORRIDGE & DAVID BLEST

Chapter 2

Materials and Methods

2.1 Zoos and Observed Animals

2.1.1 Taronga Zoo, Sydney, Australia

Taronga Zoo (33°52'S, 151°12'E) lies in the centre of the natural distribution range of koalas. Although in the centre of the city the zoo is a park like environment. Koalas have been routinely bred for several generations. The zoo population consists of zoo-born animals from Taronga Zoo or other institutions as well as a small number of wild-caught animals, which could not been released due to traumatic injuries. There are several enclosures on the zoo premises, in which the koalas are usually kept in small groups.

Eucalyptus leaves are collected daily in the Sydney area from woodland, parks and gardens by zoo staff. The quality is usually good but not always ideal, since it is dependent on season. Every day, branches of two to three different species of eucalyptus are given to the koalas. On these branches, there are young and old leaves, but a special value is set on fresh tips.

Study Group 1 – "Koala Walkabout". The breeding group was observed from 11 December 03 to 07 December 04 (Table 2.1). One wild-caught male (Ken) remained in the enclosure during the whole year of observation. The number and group composition of the females varied between two and four as they were exchanged due to breeding schedule or medical treatment (Tables 2.1 and 2.2 and Fig. 2.1). During the time of observation, a number of joeys were born, but only two emerged from the pouch.

Name	Sex	Date of Birth	In enclosure to	In enclosure from	Number of days under observation
Ken	male	Wild-caught, at Taronga since 06.11.02	b. obs.	end obs.	364
Adori	female	07.02.01 at Taronga	b. obs.	03.05.04	172
			12.07.04	end obs.	148
Carrie	female	17.04.02 at Taronga	b. obs.	10.12.03	40
			27.01.04	end obs.	126
Cooee	female	05.03.97 at Taronga	b. obs.	06.01.04	55
Felicity	female	17.04.02 at Taronga	b. obs.	09.03.04	80
Lowanna	female	07.01.93 at Taronga	10.02.04	09.03.04	30
Yindi	female	20.02.00 at Taronga	21.12.03	09.03.04	52
			10.02.04	end obs.	273

Table 2.1: Koalas observed at Koala Walkabout. b. obs. = koala was inside the enclosure before observation started; end. obs. = koala remained in enclosure until end of observation.

from	to	♯ days	♯ koalas	Individuals
11 Dec	21 Dec	10	4	Ken, Adori, Cooee, Felicity
23 Dec	05 Jan	15	5	Ken, Adori, Cooee, Felicity, Yindi
07 Jan	26 Jan	20	4	Ken, Adori, Felicity, Yindi
28 Jan	09 Feb	13	5	Ken, Adori, Carrie, Felicity, Yindi
11 Feb	08 Mar	26	5	Ken, Adori, Carrie, Felicity, Lowanna
10 Mar	03 May	55	4	Ken, Adori, Carrie, Yindi
05 May	09 Jul	66	3	Ken, Carrie, Yindi
11 Jul	07 Dec	150	4	Ken, Adori, Carrie, Yindi

Table 2.2: Group composition at Koala Walkabout during video observation.

The circular enclosure has a diameter of 12 m (113m^2). The central ground is covered with sand and surrounded by a 2 m ring of shrubs and fern trees. Four dead trees with a height of 5 m each and resting forks on different levels stand in the inner ring of the enclosure. One vase for food branches is attached to each of these trees. There is also a living tree (Silver Sheen Pittosporum *Pittosporum tenuifolium*) for resting. The enclosure is surrounded by a boardwalk that leads visitors from ground to tree level. Visitors are separated from the koalas by a low fence. Koalas sitting in the Pittosporum tree are often at eye-level with the visitors. The south side, which faces the harbour, is roof-covered and protected by a wall, providing shade and shelter from the wind and rain (Figs 2.2 and 2.3).

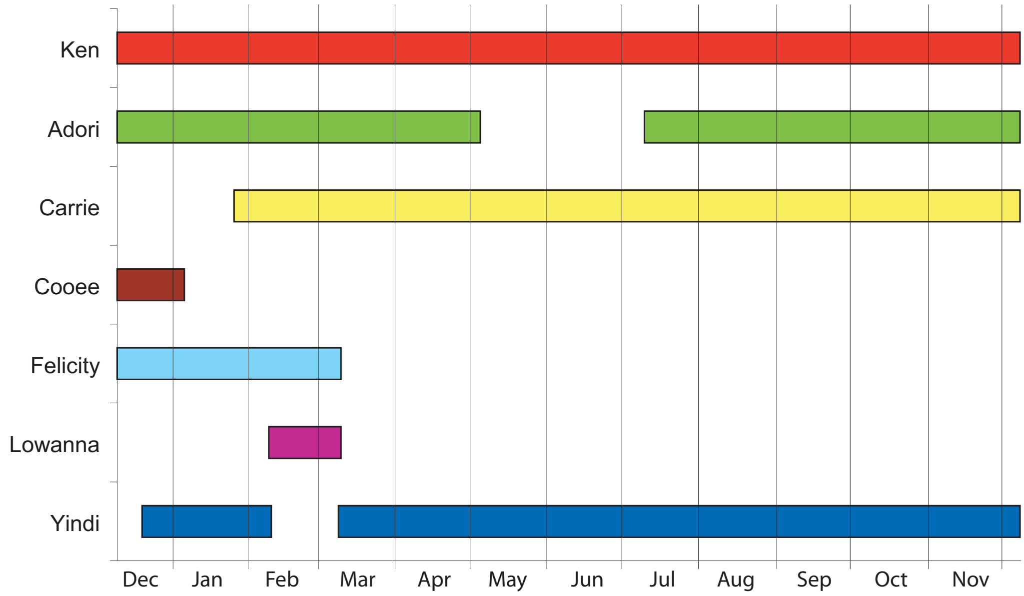

Figure 2.1: Periods when individual koalas were kept at Koala Walkabout.

The keeper usually enters the enclosure three times a day. At 7:00, the floor is cleaned and the water in the vases was changed. Between 14:00 and 15:30, the keeper enters again to remove the old food branches. New browse is presented at 15:30. After that, the keeper remaines inside the enclosure for approximately 15 minutes to give a Keeper's Talk to the visitors. There usually is no contact between keeper and koalas. If koalas are in reach of the keeper they are checked optically for their physical condition. On rare occasions, animals are touched to remove ticks or for short grooming. Animals are not forcefully removed from the trees. Some of the females approach the keeper, and then the koala is touched and, in rare cases, picked up.

Date	Event	Animals at Koala Walkabout
10 Dec 03	Pouch inspection, introduction of Felicity	Ken, Adori, Cooee, Felicity
09 Mar 04	Pouch inspection, exchange Lowanna out - Yindi in	Ken, Adori, Carrie, Felicity, Yindi, Lowanna
04 May 04	Pouch inspection, removal Adori	Ken, Adori, Carrie, Yindi
13 Jul 04	Pouch inspection	Ken, Adori, Carrie, Yindi
23 Nov 04	Pouch inspection	Ken, Adori, Carrie, Yindi

Table 2.3: List of weighing and pouch inspection at Koala Walkabout.

Figure 2.2: Koala Walkabout. Roof on Southern side of enclosure with visitor boardwalk (a); visitor's perspective of koalas resting in Pittosporum tree (b); dead trees, in the back Pittosporum tree and visitor boardwalk (c); floor of enclosure, blue water bowl underneath low palm tree (blue arrow), vases with browse on dead trees (d). Red arrows indicate koalas.

All koalas are accustomed to being caught; some of the females are trained for more extensive handling (including being carried around on the arm of the keeper and touched by visitors). At irregular intervals, but not more often than once a month, the koalas are caught and weighed on a branch attached to a spring scale (Table 2.3 and Fig. 2.4a). For the females, a pouch check is conducted, and in some cases during this study this included a pouch swab with water to sample pouch bacteria (Fig. 2.4b). This usually happenes in the morning between 07:00 and 09:00.

For the weighing three to four keepers enter the enclosure. Those koalas sitting out of arm's reach are caught by climbing up a ladder or by directing the koala downwards with a long pole. It takes up to twenty minutes to catch a koala. The females are usually more difficult to catch than the male. They snarl at the keeper but never scratch or bite. Then

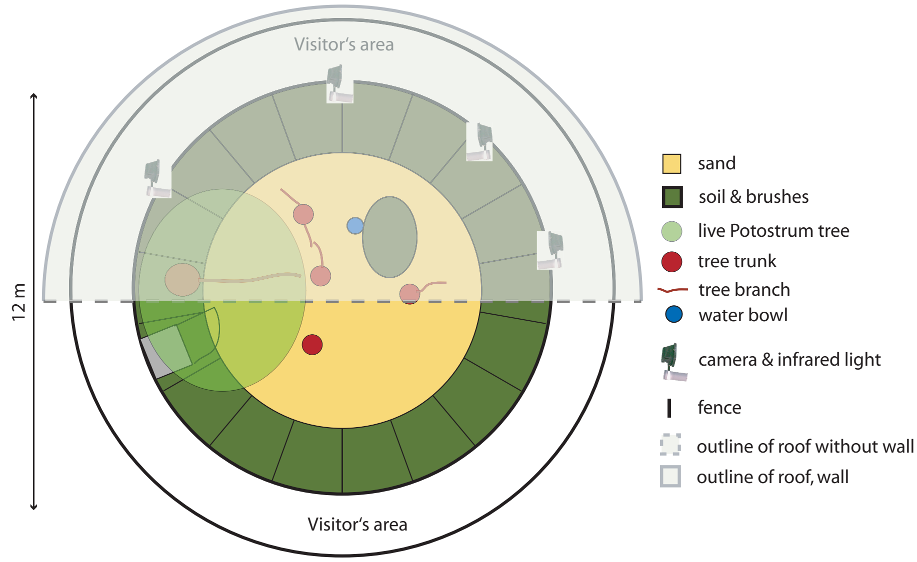

Figure 2.3: Schematic picture (on-sight) of Koala Walkabout.

Figure 2.4: Female on scale (a); pouch control in female koala, hind legs and belly of koala are visible, koala is restricted to floor (b).

the koalas are placed into a linen bag and hung in the shade, where they mostly calm down quickly, until all koalas were caught. The koalas are weighed on a spring scale, after which the male is released.

Two quokkas, *Setonix brachyrus*, Macropodidae (see Appendix F), were introduced into the walkabout in March 2004. A variety of wild birds, including common mynahs (*Acridotheres tristis*, Sturnidae, introduced), Australian raven (*Corvus coronoides*, Corvidae), laughing kookaburras (*Dacelo novaeguineae*, Alcinidae) and tawny frogmouth (*Podargus strigoides*, Podargidae) enters the enclosure. Common brushtail possums (*Trichosurus* *vulpecula*) and ringtail possums have also been observed at night (see Appendix F).

Study Group 2 – "Koala Encounter". This enclosure is located close to the main entrance and the picnic area. Visitors are allowed inside the enclosure to have photos taken standing next to a koala. No contact is allowed between visitors and koalas, but food branches are frequently rearranged by the keeper to give an unobstructed view on the animal. Photo sessions initially took place for two hours a day, usually with a "day off" every third day. Due to high numbers of visitors, the koalas were used on more consecutive days during the period of observation. There are three enclosures at the koala encounter. Bay B and C were observed between 09 December 04 and 31 January 05. At Bay B, animals were exchanged, leading to different periods of observation for different individuals (Table 2.4).

Name	Sex	Bay	observed	
			from	to
Carla	Female	B	21 Dec 04	31 Jan 05
Maggie	Female	B	18 Dec 04	31 Jan 05
Cooee	Female, mother of Coco	C	18 Dec 04	28 Jan 05
Coco	Female, daughter of Cooee	C	18 Dec 04	28 Jan 05
Georgie	Female	C	18 Dec 04	28 Jan 05

Table 2.4: Koalas observed at the Koala Encounter.

The enclosures are partly covered by a concrete roof and a sun-sail as protection from rain, wind and sun (Figs 2.6 and 2.7). There are six dead trees of 3 m height in every bay. Some of the trees are connected by horizontal trunks. The ground is covered by hard sand and there is a small band of low vegetation at the front of the enclosure.

The keepers enter the enclosure several times during the day. Between 07:00 and 08:00, the animals are checked visually and sometimes a small number of new branches is supplied. Between 08:30 and 09:00, the enclosure is cleaned. Two day old branches are removed and branches from the day before are moved to vases in the front area of the enclosure to provide additional shade. New branches are put into the vases in the back part of the enclosure. Small numbers of fresh branches are also introduced at 11:00 and 15:00, the beginning of the photo sessions, to induce activity.

During each photo session, a keeper, a photographer and her assistant are inside the enclosure. Visitors are instructed not to touch or disturb the koalas before entering. The

Figure 2.5: Frontal view of Koala Encounter with visitor's area in front.

Figure 2.6: Bay B (a) and Bay C (b) of Koala Encounter. Red arrows indicate koalas.

keeper monitors the animals, rearranges leaves for better pictures and occasionally declares a koala she considered stressed to not be available for pictures. Group size varies from single visitors to seven persons, although usually two to three people enter.

Contact between keepers and koalas is irregular but not daily. The animals are visually checked whenever possible. Since some of these koalas are hand raised and trained to be picked up and carried around, they occasionally approach the keeper and initiat contact.

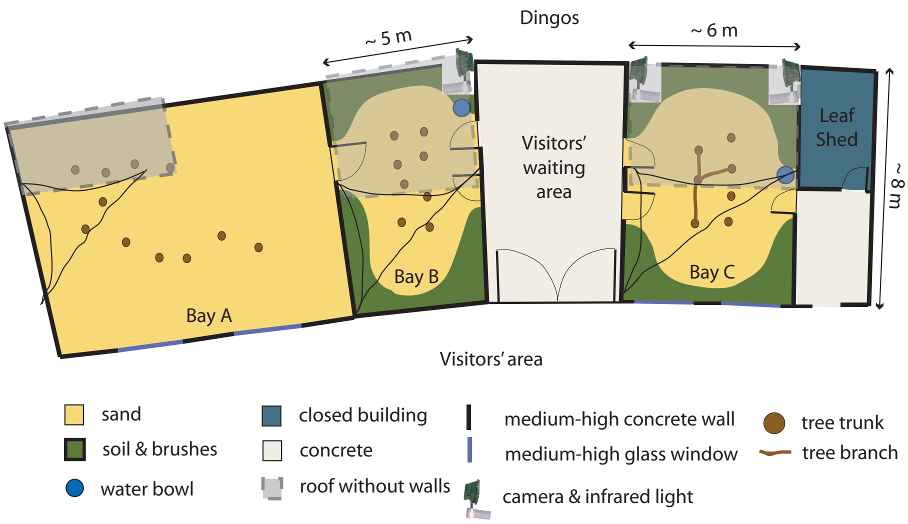

Figure 2.7: Schematic overview of Koala Encounter (including Bay A, no observation).

Usually every two weeks, the weight of the koalas is checked on a spring scale (Fig. 2.4a), but there was no weight check during the seven weeks of observation.

Few birds have been observed in the enclosures or on the walls, mainly common mynahs (*Acridotheres tristis*, Sturnidae, introduced) and peacocks (*Pavo cristatus*, Phasianidae, introduced zoo animals). Although common brushtail-possums (*Trichosurus vulpecula*, Phalangeridae) had a nest in the leaf shed adjacent to Bay C, no possums have been seen on the video tapes.

2.1.2 Zoo Duisburg, Germany

Duisburg Zoo (51°27′ N, 6°45′) is breeding koalas for more than 10 years now and is one of two European zoos with a successful breeding programme. At the time of observation, two males, three females and one joey were kept in Duisburg (Table 2.5). Two joeys were born during observation, but did not emerge from the pouch. The females and joeys are kept as a group in the display area; the two males are kept separately, one in the display area and one in the back next to the keeper's desk. This koala was not observed. Video data of six weeks each in summer 2003 and winter 2003/04 have been evaluated for this study.

Figure 2.8: Females' enclosure (a) at Duisburg Zoo; the male's enclosure (b) is on the right side, separated by a glass wall (visible on left side of picture). Red arrows indicate koalas.

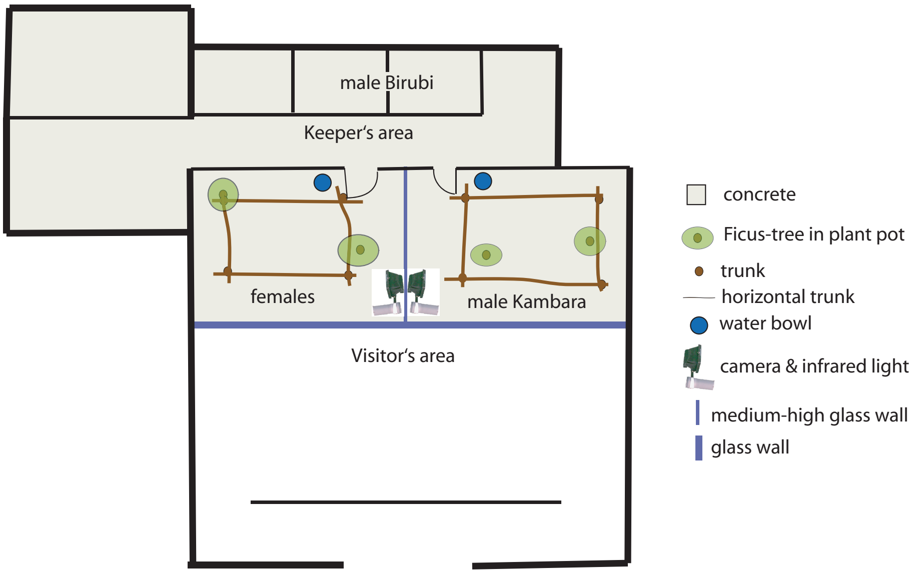

Figure 2.9: Schematic overview of the koala enlcosures at Duisburg Zoo.

Name	Sex	Date of Birth	Place of birth	Joey
Kambara	Male	20 Jul 92	San Diego	——
Yuri	Female	01 Jul 93	San Diego	Koomela, born 29 Aug 02
Kangulandai	Female	07 Jul 95	Duisbug	pouch young 24 May 03
Allora	Female	14 Feb 01	Houston	pouch young 26 Jun 03

Table 2.5: Koalas observed at Duisburg Zoo.

The display enclosures has a floor space of 5.5 m x 4 m, with a concrete floor without natural substrate and four 3 m high dead trees connected by horizontal trunks (Figs 2.8

Figure 2.10: Weighing at Duisburg Zoo. The koala's hands are secured, so the keeper cannot be scratched (a). For weighing, the koala is positioned on a fork attached to a bench scale (b).

and 2.9). Four vases for the browse for the male and five vases for the females are attached to the trunks of these trees. In addition, one *Ficus benjamini* tree is provided for the females for resting, while two are available for the male. A second tree in the females' enclosure was not accessible to the koalas at that time. For decorative reasons, different plants are attached to the wall out of reach of the koalas. Both enclosures are separated by a medium-high glass-wall, so the animals are able to see, hear and smell each other. During the cleaning in the morning, the male koala is able to see the second male in the keeper's area through the open door. They are also able to hear each other's bellowing at all times, although they generally bellow very rarely. Visitors are separated from the koalas by a sound-muffling glass front. Temperature and humidity is partly regulated but vary with outdoor conditions.

Light is provided by artificial lights as well as through sky lights made of frosted-glass. In summer, day lighting is provided from 07:00 to 22:00. The koalas experienc natural dawn, while the natural dusk is followed shortly by the switch-off of the artificial lighting.

During winter the natural day length is extended by artificial lighting. Night lighting is provided from 19:00 to 05:00. Day lighting is provided from 07:00 to 19:00. Due to the intensity of the artificial light, the koalas probably do not experience twilight.

A variety of 20 different eucalypt species is imported from plantations in Florida and sometimes South England twice a week by plane. Leaf quality is usually good to very good. Food intake and pellet production is evaluated daily by the keeper and reported to San Diego Zoo.

The keepers enters the enclosures between 08:00 and 09:00 for cleaning and feeding. Contact to the koalas at this time is rare and they are not handled. The koalas are weighed twice a week on a stationary branch fixed onto a scale (Fig. 2.10). For this the male is

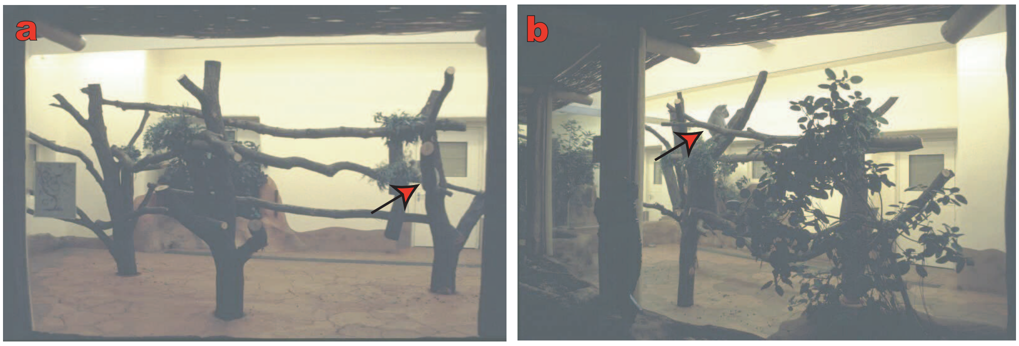

Figure 2.11: Schematic overview of the koala enlcosures at Vienna Zoo. Females' enclosure (a), the male's enclosure (b), enclosures are separated by a glass wall (visible on left side of picture b). Red arrows indicate koalas.

carried into the females' enclosure.

2.1.3 Tiergarten Schönbrunn, Vienna, Austria

Tiergarten Schönbrunn (48°12'N,16°22'E), Vienna is the oldest still existing zoological garden and one of the most modern. The koala house was opened in March 2002, exhibiting one male koala. A female koala followed in June 2002 (Table 2.6). Both koalas are kept separately in indoor enclosures very similar to Duisburg Zoo. Despite several breeding attempts, so far no joey has been born in Vienna. Video data was evaluated for two periods of six weeks each in summer 2004 and winter 2004/05 for a norm-actogram as well as for six weeks in summer 2005 when weighing times were changed.

The floor space of the enclosures is 5.5 m x 4 m. The floor is concrete with no natural substrate (Figs 2.11 and 2.12). Three 2.5 m high dead trees, which are connected as a triangle by two horizontal trunks in each direction, are provided. Five vases for the browse for the male and four vases for the females are attached to the trunks of these trees. There are three small areas with vegetation and natural soil in each enclosure. The enclosures are separated by a medium-high glass wall which allows the koalas to see, hear and smell each other. Since 2004, this glass wall has been opened for short periods of time to allow the koalas access to each other. In addition to artificial lights natural light is provided through large skylights. Twilight is simulated by five changes in light intensity. Until 2004 temperature and humidity were controlled and stabilized at 22°C ± 1°C and 60% humidity.

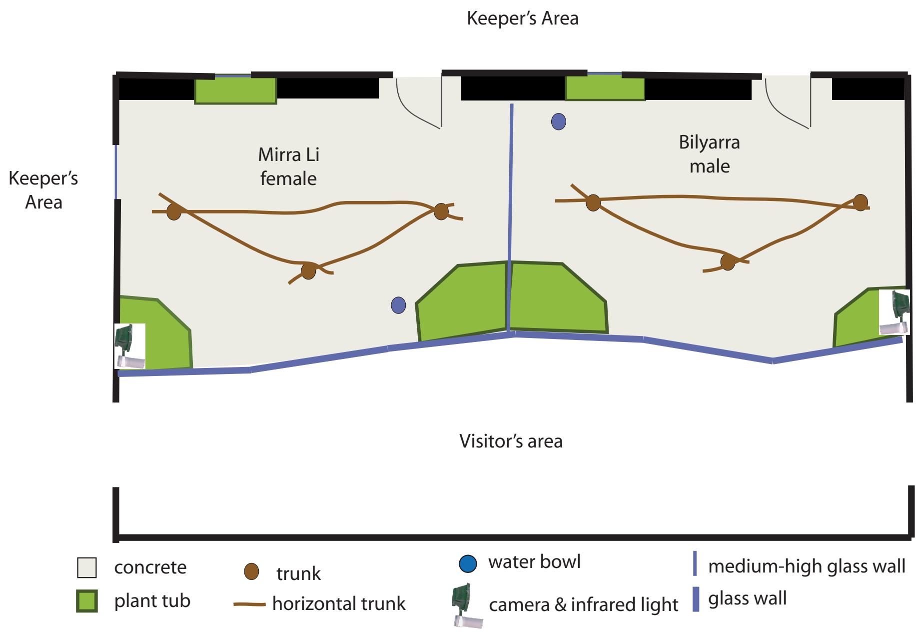

Figure 2.12: Schematic overview of the koala enlcosures at Vienna Zoo.

Name	Sex	Date of Birth	Place of birth	Arrival Schönbrunn
Bilyarra	Male	27 May 98	Duisburg	13 Mar 02
Mirra Li	Female	24 Feb 02	Houston	13 Jun 02

Table 2.6: Koalas observed at Tiergarten Schönbrunn.

Twice a week, about 50 kg of eucalyptus leaves are imported from a plantation in South England by plane. To provide variety and cater for the changing wants of the koalas, around 30 different eucalypt species are supplied, four to five at a time. Leaf quality is usually good to very good. As in Duisburg Zoo, food intake and pellet production was evaluated daily by the keeper and reported to San Diego Zoo.

Between 8:00 and 9:30, the enclosure is entered by the keeper for cleaning. During this time, the koalas are checked visually and handled to check claws and ears. Regularly, the animals, especially the female, are picked up and carried around or taken out of the enclosure for a couple of minutes. The female often approaches the keeper and signals to be picked up by her. After cleaning, a small number of new branches is provided in one or two of the vases. At 10:15, the animals are weighed on a stationary branch. After being put back on a sitting branch, the remaining browse is given. At approximately 15:45, food is checked and, if necessary, additional browse is given.

Visitors are separated by a sound-muffling glass front. If the noise level in the visitors area is too loud or people knock on the glass, they are admonished by a recorded voice. Flash photography is not permitted. Koalas and visitors are under random video surveillance by the keeper.

2.2 Video Observation

All enclosures were videographed for 24 hours a day with a time lapse video recorder. During the night, infrared lights (152 cascaded infrared diodes SFH 485, wavelength 880 nm, Siemens) were used (Fig. 2.13b). This wavelength cannot be seen by mammals and should therefore not influence their behaviour (Eckert et al. 1993). At Taronga Zoo and Duisburg Zoo, self-made infrared lights were used (© AK NCR, Frankfurt University), while professional lights were used in Vienna (© Bosch).

At Taronga Zoo black/white, infrared sensitive cameras (CCD, AD-502A, lenses varied between 4 and 12 mm, Watec Comp.) were used. At Koala Walkabout four cameras with lenses varying between 4 and 12 mm covered overlapping areas of the enclosure. The cameras were installed about 4 m above ground (Fig. 2.13a). At Koala Encounter, one camera was used for Bay B and two for Bay C (Figs 2.3 and 2.7. Both cameras were installed about 3 m above ground.

At Duisburg Zoo the female's enclosure was equipped with two cameras (CCD, 116750, Conrad Electronics), a 12 mm telelens at a height of 3 m to observe the mother with her joey on their favourite spot and a 6 mm wide angle for the complete enclosure 5 m above ground 2.9. For the male, a 6 mm wide angle lens was used at a height of 5 m. Here, the same infrared lights were used as in Sydney.

In Sydney and Duisburg, the single camera signals were combined into one picture with a black/white quad processor. In Sydney, pictures were recorded with a XPOSE QV3053 time lapse video recorder taking two pictures per second, and in Duisburg, with a Panasonic AG-6720E time lapse video recorder taking 1.5 pictures per second.

At Tierpark Schönbrunn, a black/white, infrared sensitive Bosch digital video observation system including cameras and infrared lights was used. One camera (3 m above ground) per enclosure was connected to a motion detector, so the speed of the recording was increased whenever the animal was active. Pictures were stored in single archives and analysed using the picture archive programme BoVis 6.0 (Bosch 2002).

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Figure 2.13: Self-made infra-red light (left) and video camera (right) at Koala Encounter (a). At Koala Walkabout both were installed on top of the visitor's boardwalk (b).

2.3 Analysis of video tapes

2.3.1 Behavioural categories

After an appropriate period of direct observations, two behaviours were chosen for analysis: feeding and locomotion. Other behaviours like grooming, drinking and social interactions have either been rare or were not reliably recognizable on the video pictures. It was noted whether feeding or locomotion was observed within a five minute interval. In some cases, both behaviours occurred. To assess general activity, each behaviour was given a relative activity level. This level was not calibrated with metabolic rate, but defined by the observer in relation to the other behaviours. Data loss is given an activity level of zero. The following behaviours have been noted (activity level in brackets):

Inactive	(1)	The koala is resting or shows low activity like grooming or a change of position without changing place.
Feeding	(4)	Koala is feeding for more than two minutes on eucalypt branches.
Loc 1	(3)	Koala is changing its place but moves not more then two body lengths and is not feeding.
Loc 2	(5)	Koala moves more than two body lengths but less than three minutes.
Loc 3	(7)	Koala moves at least three minutes during the five minute interval.
F&L	(6)	Due to the length of the interval, feeding and locomotion was sometimes observed in the same interval. In this case, for analysis, the interval was included in both behaviours.

2.3.2 Places

Some places, which seemed to be of significance for the koalas, have been analysed similar to the behaviour categories. Due to the differences between the zoos, not all of them could be compared to each other.

On ground	Observed in all zoos; koala was on the floor of the enclosure with all four legs.
In tree	Observed at the Koala Walkabout, Taronga Zoo; koala was in the Pittosporum tree underneath the canopy either close to the trunk or on a small branch connecting the tree to the dead trees.
In canopy	Observed at the Koala Walkabout, Taronga Zoo; koala is inside the canopy of the Pittosporum tree.

2.4 Analysis of data

2.4.1 General data analysis

All data were collected using Microsoft Excel. Mean values, standard deviation and time budgets have been calculated here. If not mentioned otherwise diagrams have been plotted using Excel and have been graphically processed in Adobe Illustrator CS.

Data have been collected in two time zones. The following abbreviations can be found in the text and diagrams:

AEST	Australian Eastern Standard Time (GMT +10:00)
AEDT	Australian Eastern Daylight-Saving Time (GMT +11:00)
CET	Central European Time (GMT +1:00)
CEST	Central European Summer Time (GMT +2:00)

Times of sunrise, sunset and civil twilight have been obtained from the US Naval Observatory, Washington DC. Temperature data for Sydney has been provided by the Australian Bureau of Meteorology (BOM).

2.4.2 Chrono-ethograms

To analyse circadian and seasonal rhythms chrono-ethograms have been plotted using a self-developed script (© Tronje Krop, Technische Universität Darmstadt) for awk (Aho

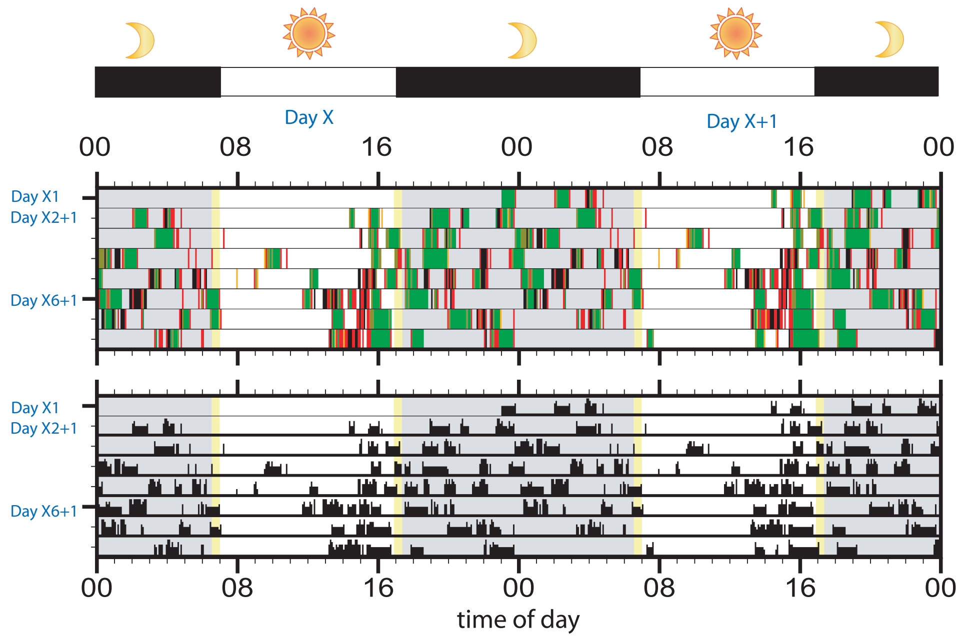

Figure 2.14: Two double-plot chrono-ethograms of a koala.
Ethogram on top shows behaviour categories with different colours, actogram below shows relative activity levels indicated by height of columns. Light regime can be shown either using a black/white bar on top of the actogram or using a profile underlying the behaviour data, in this case day (white), night (grey) and twilight (yellow). The first day in the line (Day X) is followed by the second day (Day X+1); this second day is repeated as the first half of the second line.

et al. 1988) and afterwards graphically processed in Adobe Illustrator CS. Double-plot chrono-ethograms show a series of 48 consecutive hours per line plotted, where the last 24 hours of the first line is repeated as the first 24 hours in the second line and so on (Fig. 2.14).

Chrono-actograms were used to give an overview on general activity based on the relative activity levels for the behaviour. They include every observed behaviour category. For fine analysis, selected behaviours have been plotted in chrono-ethograms.

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2.4.3 Period lengths and power spectrum

Data were examined for their relative amounts of rhythmic components by plotting the period length τ as Lomb-Scargle-Periodogram (power spectrum) (Ruf 1999). The used formula is based on Fast-Fourier-Transformation (FFT), but accounts for unevenly spaced data. Periods were tested for significance (p=0.05) with a Chi^2-threshold value, which is indicated by a horizontal line in the power spectrum. Calculations and plotting were performed by a self-developed script (© Thomas Gbenro, Universität Frankfurt) for R (R Development Core Team 2006).

2.4.4 Activity profiles

Activity profiles show an average profile of activity during a day on a 24 hour scale. They have been calculated as the mean number of intervals showing certain behaviours at a particular time of day. In the case of locomotion, all three defined levels of locomotion have been combined using the following calculation:

Loc1	one count per interval
Loc2	two counts per interval
Loc3	three counts per interval

2.4.5 Time budget and day:night ratio

The total proportion of each behaviour per day was represented both in percentage and total time. To test if a behaviour was more often observed during the night, the relation of day to night length had to be taken into account, especially when comparing summer and winter. The day:night ratio *r* was calculated with a self-developed script (© Tronje Krop, Technische Universität Darmstadt) for awk (Aho *et al.* 1988) using the following formula:

$\bar{c}_d = \frac{c_d}{t_d}$	$\bar{c}_n = \frac{c_n}{t_n}$
$c_d =$counts per day	$c_n =$counts per night
$t_d =$time per day [hour]	$t_n =$time per night [hour]

$$r(\bar{c}_d, \bar{c}_n) = \begin{cases} \textit{undefined} & \text{for} \quad \bar{c}_d = 0, \bar{c}_n = 0 \\ -1 & \text{for} \quad \bar{c}_d = 0, \bar{c}_n \neq 0 \\ 1 & \text{for} \quad \bar{c}_d \neq 0, \bar{c}_n = 0 \\ \frac{\bar{c}_d/\bar{c}_n - 1}{\bar{c}_d/\bar{c}_n + 1} & \text{for} \quad \bar{c}_d \neq 0, \bar{c}_n \neq 0 \end{cases}$$

In Sydney night is defined as the time between sunset and sunrise including civil twilight. In Vienna and Duisburg night is defined as the time in which the day lighting is turned off. Natural twilight as experienced by the koalas was not taken into consideration for the day:night ratio.

2.4.6 PSTH-graphs

Post- or Pre-stimulus-time-histograms (PSTH) show the effect of an event (stimulus) on the animal. The mean number of intervals in which feeding or locomotion had been observed was calculated and plotted on a time axis usually covering 120 minutes before and 120 minutes after the stimulus to see whether there was anticipatory behaviour or the behaviour was triggered by the stimulus.

PSTH-graphs were used to analyse

- the influence of natural light, and
- the influence of keeper activity and contact.

2.5 Statistical analysis and error estimation

All statistical tests were calculated using SPSS 11.0 for Windows (SPSS Inc. 2001). Data were tested for normal distribution using the Kolmogorov-Smirnov-test. Samples with normal distribution were tested for significant differences using either t-tests or repeated measurement univariate ANOVA with Tuckey Posthoc test. If data were not distributed normally, they were tested with Friedman ANOVA and the Kolmogorov-Smirnov-Z test. p is given for each diagram and in some cases indicated by asterisks as * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$. All statistical data not given in the result chapter can be found in Appendix G.

For Koala Walkabout, Taronga Zoo, 363 days of observation have been analysed to gain information about seasonal variations in day-night rhythms. For comparison between zoos, six weeks in summer and six weeks in winter have been analysed for each group. If possible, the time around the summer and winter solstice was chosen. Due to technical reasons, this was not possible in Duisburg during winter. At Koala Walkabout, Taronga Zoo, females were exchanged frequently due to the breeding plan. For some of the analysis, data of different females between December and January have been pooled to increase the sample size. At every zoo, one male has been observed, but due to the small sample size, no general sex differences in the behaviour can be analysed.

Whether we consider the uncouth and remarkable form of its body, which is particularly awkward and unyielding or its strange physiognomy and manner of living, ... they have little either in their character or appearance to interest the Naturalist or Philosopher.
GEORG PERRY (1810)

Chapter 3

Results

3.1 Sydney Koala Walkabout (Taronga Zoo)

3.1.1 Chronoethogram of total activity

The general time pattern was similar in all koalas and did not change significantly during the year (Figs 3.1, 3.2, 3.3 and 3.4). It showed a mainly, but not exclusively nocturnal habit: most feeding and locomotor activity was observed during the night, frequently interrupted by resting bouts. In the morning all koalas were resting. Activity, particularly locomotor activity, became more frequent during the day, especially in the afternoon.

A clear onset of feeding activity was observed during the Keeper's Talk (provision of fresh browse and short talk by keeper to visitors, for further details see **??**) at 15:30 (14:30 during daylight-saving time, AEDT), precisely after fresh browse had been provided by the keeper (less clear in *Yindi*, Fig. 3.2). In summer, several feeding bouts followed during the afternoon. However, these varied between individuals. In all koalas feeding bouts were frequent during the night.

Locomotor activity in most koalas anticipated on many days the Keeper's Talk at 15:30. It began at different times and ended with the onset of feeding at the Keeper's Talk. More intensive locomotor activity (Loc3) could also be observed during night with a concentration before and around dawn (*Yindi*, Fig. 3.2 and *Carrie*, Fig. 3.4). Locomotion bouts in the morning and around noon were short and without obvious pattern.

Although the general day-night pattern remained clear throughout the complete year, there were significant differences in the pattern of feeding bouts in the afternoon and at dusk. Mostly the koalas started to feed shortly after the fresh browse was introduced at the beginning of the Keeper's Talk. This feeding bout was of comparatively long duration. Along consecutive days these feeding bouts appeared like a band. This band was strongest in the male *Ken* and weakest in the female *Yindi*, who did not feed during the

Keeper's Talk on most days, though locomotor activity was regular. The feeding patterns changed during the year. These changes will now be described in detail for each koala.

In *Ken* the band at dusk changed with seasons. Between December and February, there was a broad band of feeding between 17:00 and 19:00 (Fig. 3.1, a). At the end of February, this band met dusk (Fig. 3.1, b). The feeding bouts lay closer together now and the onset of the bouts were related to dusk, but slowly moved forward to 17:00, the earlier onset of the bouts. This was especially obvious in one freerunning rhythm in the second half of March which started in the night and moved toward 17:00 (Fig. 3.1, c). From April on, the sun set before 18:00. The second feeding band now merged with the band at the Keeper's Talk (Fig. 3.1, d). In late August, the band appeared again at dusk and the band at the Keeper's Talk lost strength (Fig. 3.1, e). For about one month there was concentrated feeding around dusk. There were several freeruns which connected the Keeper's Talk with dusk. At the beginning of October both bands basically disappeared (Fig. 3.1, f), but in mid October the band at the Keeper's Talk was strong again. There was one last freerun to dusk. In November a feeding band in the afternoon was seen as in the summer before (Fig. 3.1, g).

In *Yindi*, a strong band of feeding activity was seen at dusk (Fig. 3.2). She fed on almost every day, so this was her main feeding time. Different to *Ken*, major seasonal changes were visible in the band at the Keeper's Talk. During her first stay at Koala Walkabout it was not possible to clearly discriminate *Yindi* from the other koalas, especially from *Felicity* who was the same size (Fig. 3.2, a). Therefore this period was not analysed in detail. When *Yindi* returned to Koala Walkabout, there were two activity bands, one at the Keeper's Talk and one at dusk, changing with sunset (Fig. 3.2, b). In April the band at the Keeper's Talk disappeared and the band at dusk became stronger (Fig. 3.2, c). Until mid October it was the only band in feeding and clearly related to sunset. Feeding at the Keeper's Talk was rare. From November on there was a band at Keeper's Talk again, but the one at dusk did not loose its strength (Fig. 3.2, d).

Legend for figures 3.1, 3.2, 3.3 and 3.4: Continuous double-plotted chronoethogram for feeding and locomotor activity from December 2003 to December 2004. Green bars = feeding , red bars = locomotor activity; vertical blue line = morning cleaning, vertical green line = Keeper's Talk. Background colours: grey = night, yellow = twilight. Letters on the right margin indicate periods referred to in the text.

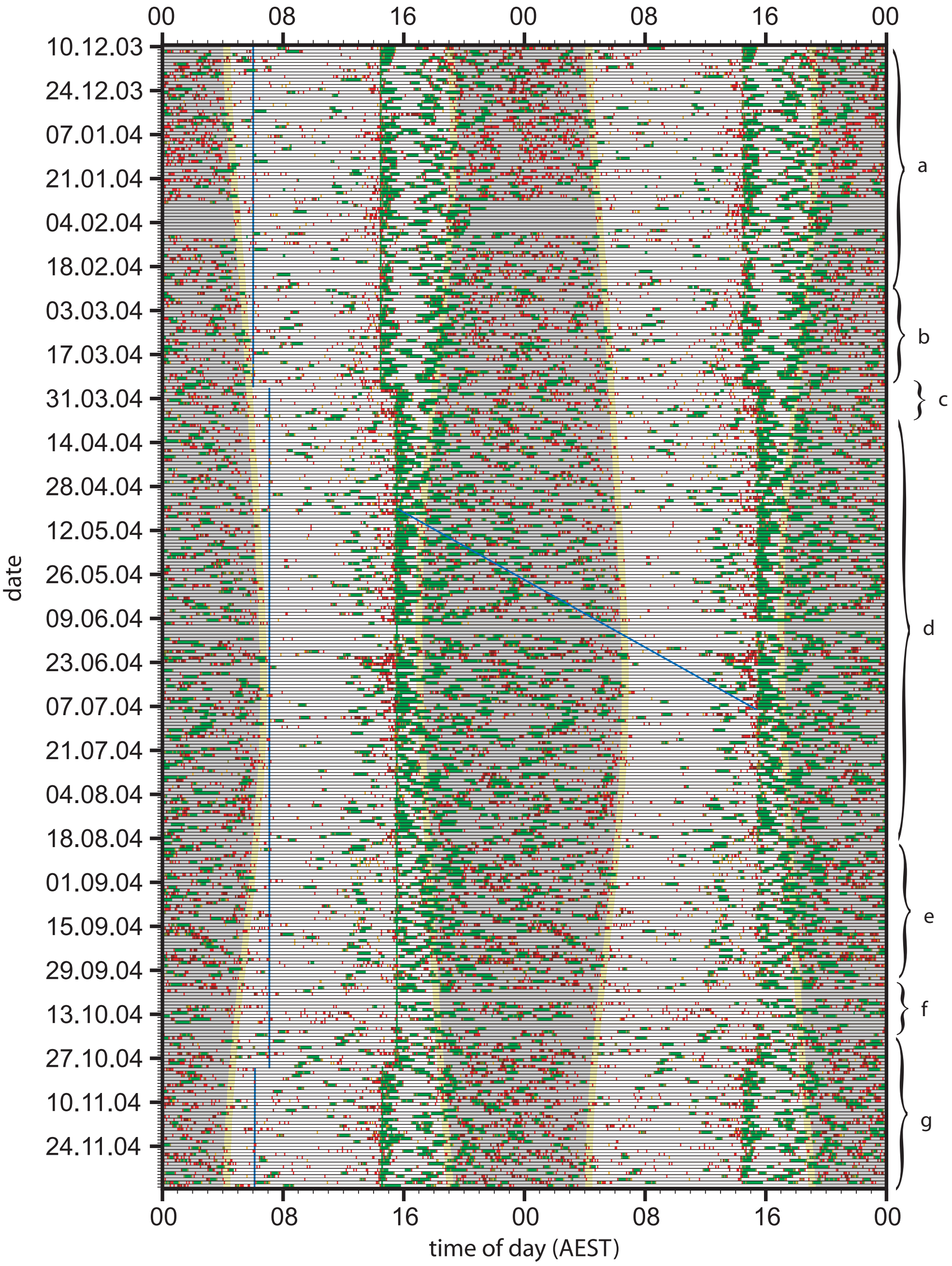

Figure 3.1: Feeding and locomotior activity for the male Ken for one complete year.
Diagonal blue line indicates freerunning rhythm referred to in text. For further details see page 50. The male koala *Ken* was kept at Koala Walkabout during the complete observation period.
Both behaviours display in the chronoethogram show an obvious circadian pattern. Feeding is concentrated after the Keeper's Talk, around dusk and at night, especially in the first part. Locomotor activity occurred mainly during the night and before the Keeper's Talk. In the morning locomotor activity was rare and unevenly distributed. This pattern did not change significantly over the year.

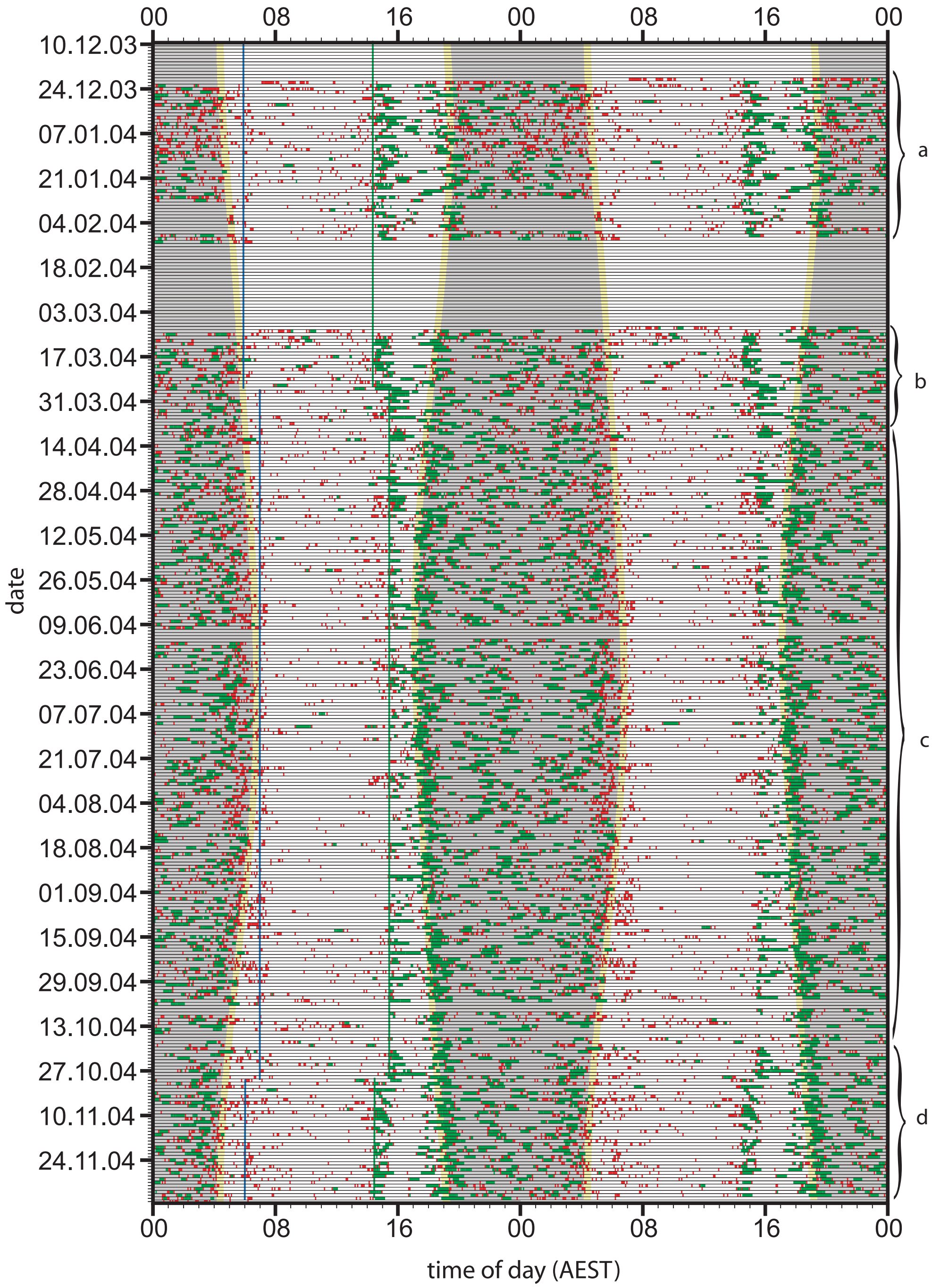

Figure 3.2: Feeding and locomotor activity for the female *Yindi* for one complete year.
For details see page 50. *Yindi* was moved to Koala Encounter on 21 December 2003 from the Education Centre. She was exchanged for the female *Lowanna* on 10 February 2004, but returned on 09 March 2004. Her joey was born around 15 March 2004 and started to leave the pouch in September 2004.
Both behaviours display in the chronoethogram show an obvious circadian pattern. Feeding is concentrated around dusk and in the night. There is almost no feeding during the day, with exception of a weak band beginning at the Keeper's Talk. It is stronger in summer than in winter. Locomotor activity is frequent during the complete day with a concentration around dawn. In winter, the discrimination between day and night is stronger than in summer.

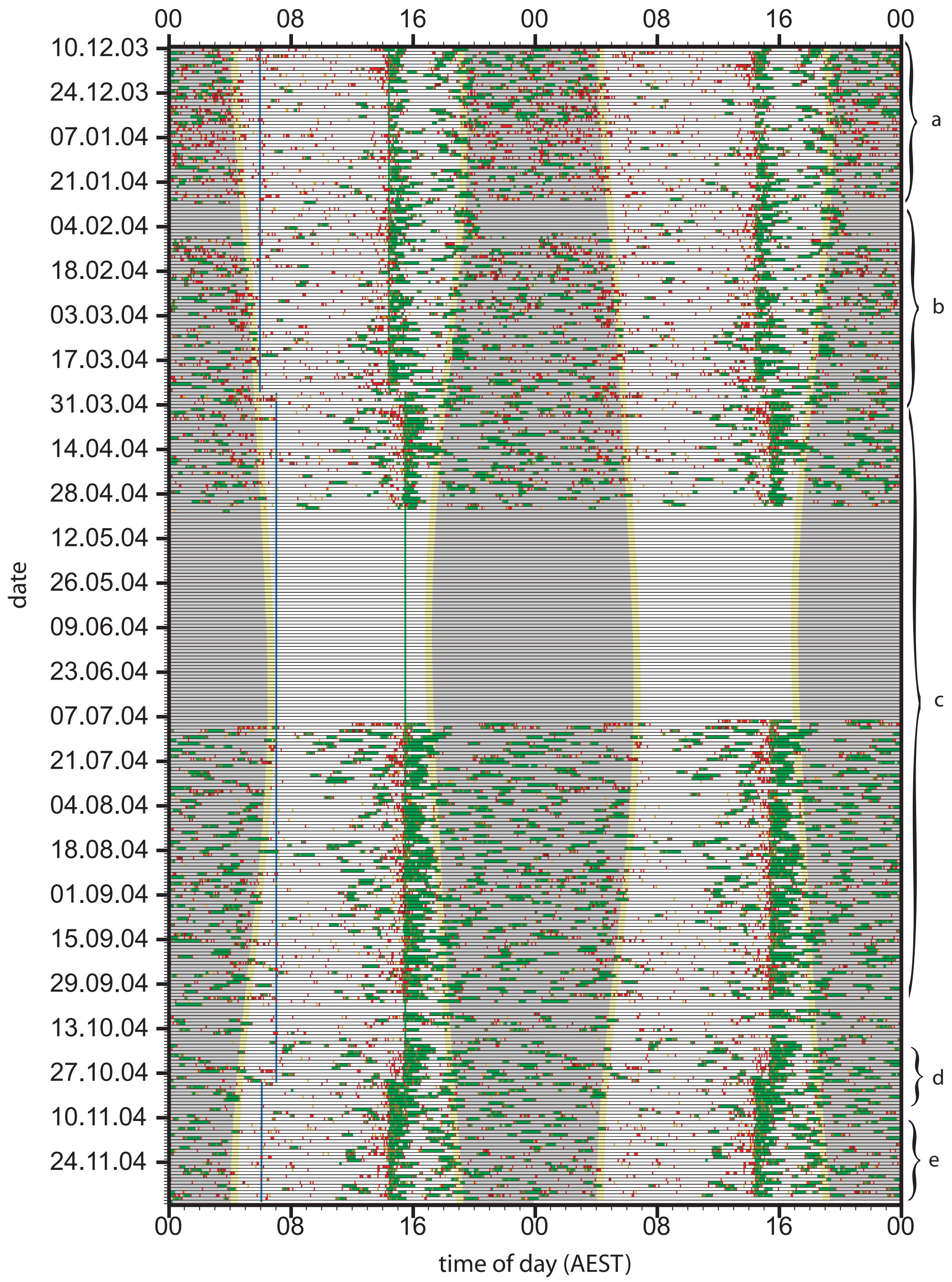

Figure 3.3: Feeding and locomotor activity for the female *Adori* for one complete year.
For details see page 50. *Adori* gave birth around 15 November 2003. The joey was found dead on 19 April 2004 and *Adori* was removed to the veterinarian station on 04 May 2004. She returned on 12 July 2004 and gave birth to a joey around 15 November 2004.
Both behaviours display in the chronoethogram show an obvious circadian pattern. Feeding is concentrated to the night and shows a strong band beginning at the Keeper's Talk. Locomotor activity is more frequent during the night, especially in winter, with a concentration around the Keeper's Talk and dawn.

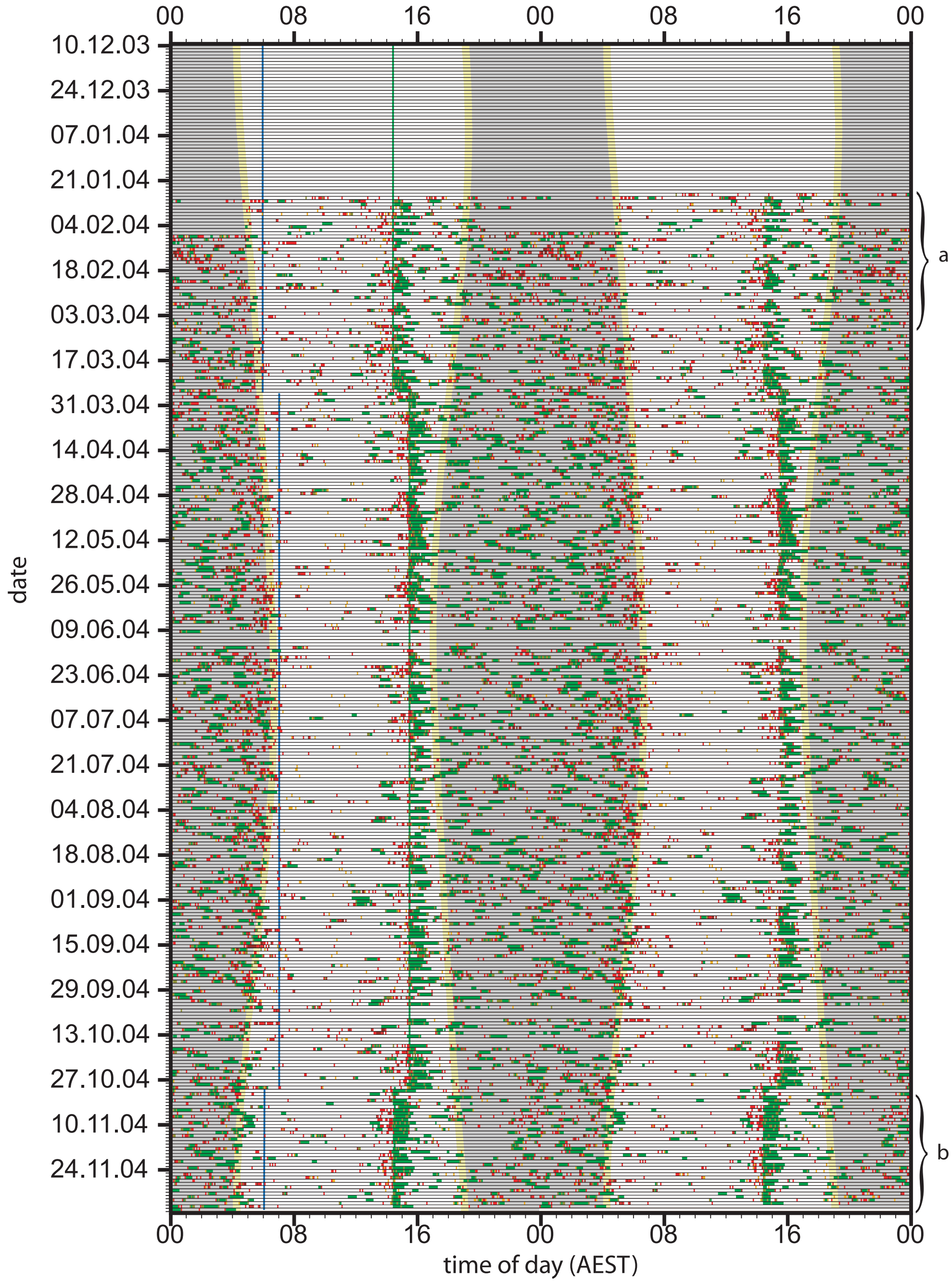

Figure 3.4: Feeding and locomotor activity for the female *Carrie* for one complete year.

For details see page 50.*Carrie* was moved to the Koala Walkabout on 27 January 2004 after she had lost a joey on 06 January 2004. She again gave birth around 02 March 2004, but lost the joey on the beginning of April. A third joey was born around 25 May 2004.

Both behaviours displayed in the chronoethogram show an obvious circadian pattern. Feeding and locomotor activity was concentrated to the night and around the Keeper's Talk. Locomotor activity was more common in the second half of the night and particularly around dawn. In winter, activity was rare in the morning.

In *Adori*, the feeding band at the Keeper's Talk was strong during the complete year. In summer and spring there was some feeding in the evening between 18:00 and 20:00 (Fig. 3.3, a). In February and March, the second feeding band was somewhat related to dusk, but this band was not very strong and feeding was not observed daily (Fig. 3.3, b). From April to September there was only the band at the Keeper's Talk (Fig. 3.3, c). In October, feeding again was observed during dusk for a short while (Fig. 3, d) before a band in the afternoon appeared again (Fig. 3.3, e).

Carrie displayed a strong feeding band at the Keeper's Talk throughout the complete year (Fig. 3.4). In both summers there were additional feeding bouts in the afternoon (Fig. 3.4, a,b), but feeding seemed not to be related to dusk.

During the night, frequent activity bouts have been observed in all koalas, but without any distinct bands. Feeding ceased with sunrise, but in locomotor activity there were differences between individuals and seasons. In *Ken* locomotor activity ceased with sunrise in winter too, but in summer there was more locomotor activity observed during daytime than in winter (Fig. 3.1). Generally, activity in the summer nights was more concentrated and activity bouts were closer together. In *Yindi*, locomotor activity ceased with sunrise in winter too, but in summer there was frequent locomotor activity until about 08:00 (Fig. 3.2). In the last two hours before dawn there was an increase in locomotor activity, especially in winter. In *Adori*, locomotor activity ceased with daylight during the complete year (Fig. 3.3). The same was the case in *Carrie*, but as in *Yindi* there was a band of locomotor activity shortly before sunrise (Fig. 3.4).

At night, freeruns in feeding have been observed during the complete year. Some of these freeruns lasted only a few days and ranged only over three or four hours, but others lasted several weeks and extended over the complete night or longer. In *Ken* such freeruns were particularly obvious during winter when activity started with the Keeper's Talk and feeding ended shortly before dusk (Fig. 3.1). Some of these freeruns were even displayed as activity bouts during daytime, though there were gaps of several hours and days between single bouts. In most freeruns, τ was longer than 24 h, but in some freeruns τ shorter was than 24 h, especially in *Yindi* (Fig. 3.2).

3.1.2 Time budgets and day:night ratios of behaviour

The koalas spent most of the 24 hours resting (Fig. 3.5). *Ken* was significantly more active than the females. He rested on average for 18 h 8 min per day, while the females had an average resting time of 19 h 6 min per day. Feeding was the most common activity, accounting on average for 3 h 6 min per day in *Ken* and 2 h 30 min in the females.

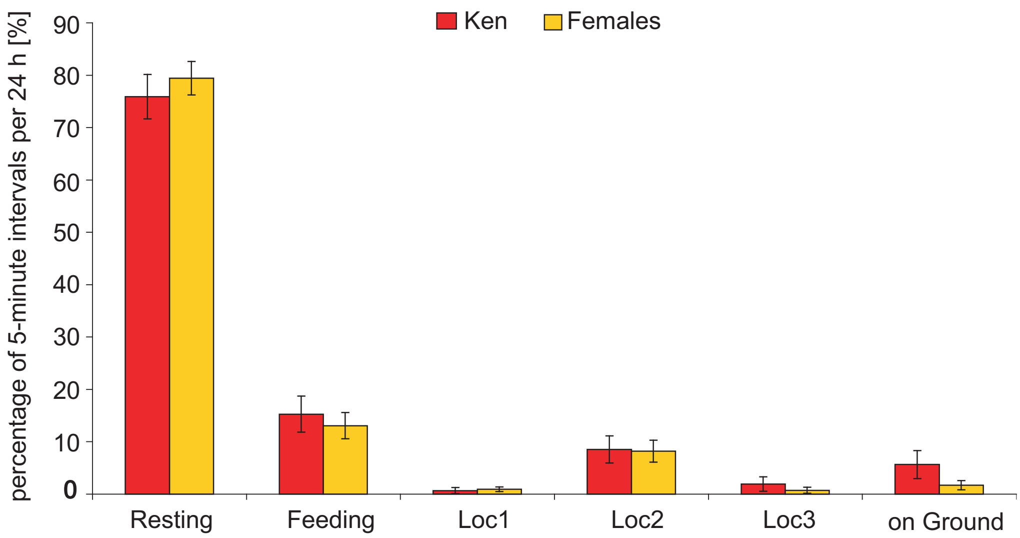

Figure 3.5: Average daily time budget of different behaviours in *Ken* and the females during one year. Percentage of 5 min observation intervals per 24 hours; bars indicate standard deviation between days. Feeding and Loc2 have been regularly observed in one interval. In this case, the interval was counted for both behaviours, so the sum of all behaviour is bigger than 100%. Presence on ground is counted independently. Female koalas and their number varied between two and four females during the observation period (see chapter 2, table 2.2). Data have not been tested statistically.
The biggest part of the day was spent resting. Feeding was the activity most often observed, Loc2 was the most common kind of locomotor activity. Loc1 and Loc3 were rare behaviours with high standard deviations. *Ken* was significantly more active than the females, spending more time feeding, Loc3 and on the ground.

The most common locomotor activity was Loc2, usually used for changing location or checking food vases. Loc1 was rare and more common in the females than in *Ken*. Loc3, which is basically wandering, and presence on ground was almost three times more often observed in *Ken* than in the females. Loc1 and Loc2 lasted less than 5 minutes, but due to the sampling interval of five minutes every bout was recorded as a five-minute-bout. Therefore the duration given here may be longer than the time actually spent with this behaviour and the total of all behaviours adds up to more than 100%.

Resting was slightly more often observed during the daytime, without any differences between *Ken* and the females (Fig. 3.6). However, the koalas were not strictly nocturnal, but displayed a considerable part of their activity during the day. Feeding was more often displayed during the night in the females than in *Ken*. *Yindi* had a day:night ratio of -0.71 $\pm$ 0.300, which shows that she rarely fed during daytime. Loc2 and Loc3 were also more often observed during the night in all koalas, while Loc1 was not as clear. Figure 3.6 shows that Loc1 more often displayed during the night, but this varied strongly between days. Loc1 and Loc3 were also not observed daily. Both behaviours were more common

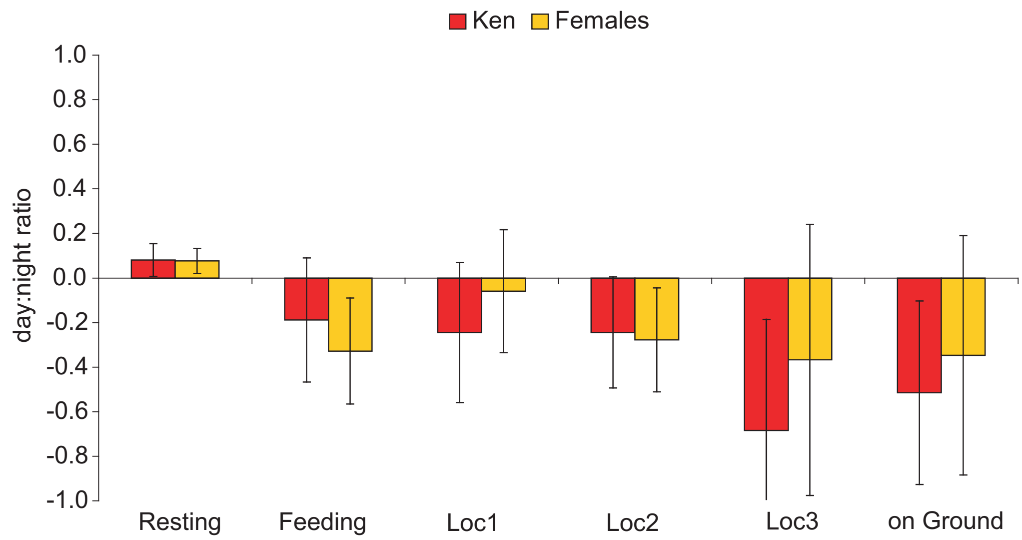

Figure 3.6: Average day:night ratios of different behaviours in *Ken* and the females over one year. Positive values indicate that behaviour was more often observed during the day, negative value that it was more often observed during the night. Bars indicate standard deviation between days. For further details see Fig. 3.5.
Resting was the only behaviour that was slightly more often observed during daytime. Feeding and locomotor activity were more often observed during the night. Thus the koalas were not strictly nocturnal. Feeding was significantly more common during the night in the females than in *Ken*, Loc1, Loc3 and presence on the ground were more common during the night in *Ken* than in the females.

during the night in *Ken* than in the females. Presence on the ground showed the same pattern as Loc3.

3.1.3 Seasonal variations

Seasonal patterns in time budget were especially obvious in resting and feeding. This will be analysed in the following. *Ken* has been analysed separately from the females to account for possible sexual differences in behaviour.

Resting. The chronoethograms for the complete year (Figs 3.1, 3.2, 3.3 and 3.4) show that resting had a strong relation to light. In *Ken*, total resting times per day were slightly shorter in May and June (autumn, early winter) than in most of the remaining year (Fig. 3.7a). In the females, the seasonal variation was not as strong (Fig. 3.7b). The highest levels of resting occurred for both sexes in February. Levels were also high in October and November (spring), especially in the females, of which two had joeys at this time. Throughout the whole year the koalas rested slightly more during the day (Fig. 3.7c). This was particularly strong in Southern summer (December to February), but did not

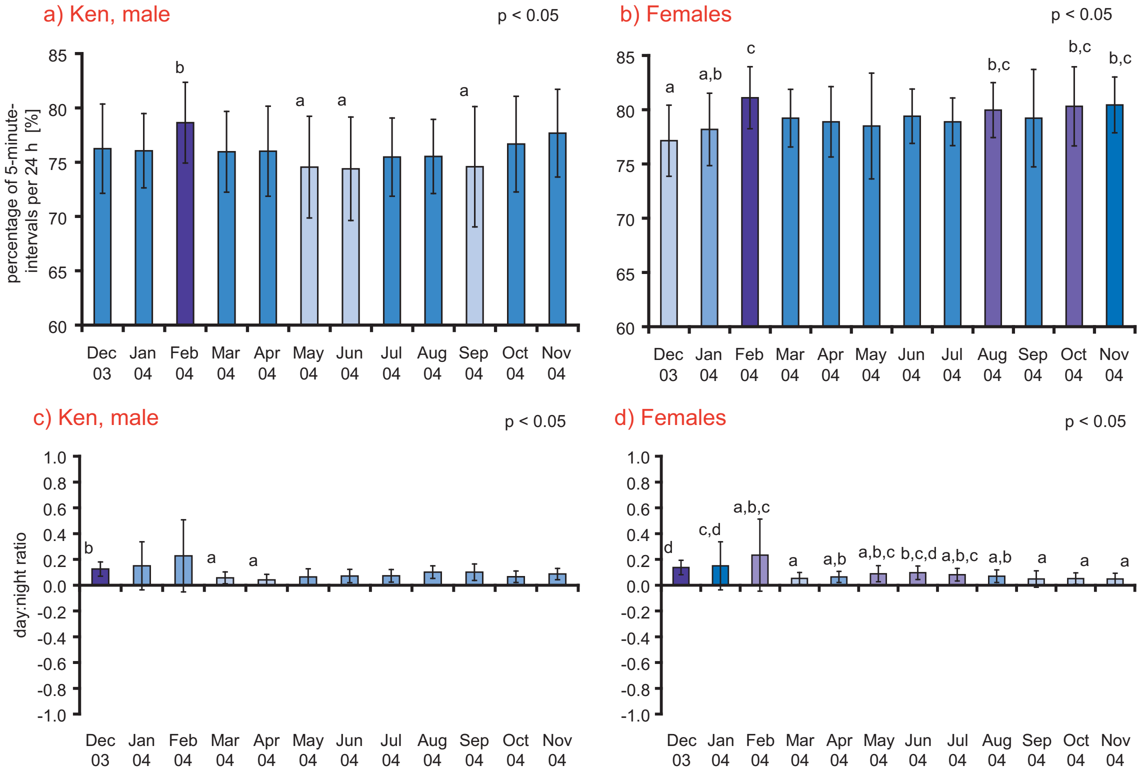

Figure 3.7: Average monthly resting time and day:night ratio in *Ken* and the females during the year. Upper panel: Percentage of 5 min observation intervals per 24 hours; bars indicate standard deviation between. Lower panel: Positive values indicate that behaviour was more often observed during the day, negative value that is was more often observed during the night. Bars indicate standard deviation between days. Letters and colours indicate significant differences between months. Female koalas and their number varied between two and four females during the observation period.
Resting levels were highest in February. In *Ken*, levels were lowest in May and June and increased slightly afterwards. In the females resting levels were generally higher than in *Ken* and did not decrease as much towards winter. Resting was observed more often at daytime during the complete year. In the females there was relatively more resting during the day between May and July, though the nights were longer.

vary much for the remaining year. Nevertheless in the short winter days between May and July, there was relatively more resting during the day (Fig. 3.7d).

Feeding. Feeding showed the clearest seasonal variation. In *Ken*, total time feeding was lower between December and February (summer), increased until May and decreased again until October/November (Fig. 3.8a). In the females values were also low between December and February (summer) and increased until April, but remained high until the end of observation in early December (Fig. 3.8b).

The day:night ratio of feeding was negative with exception of February. The most

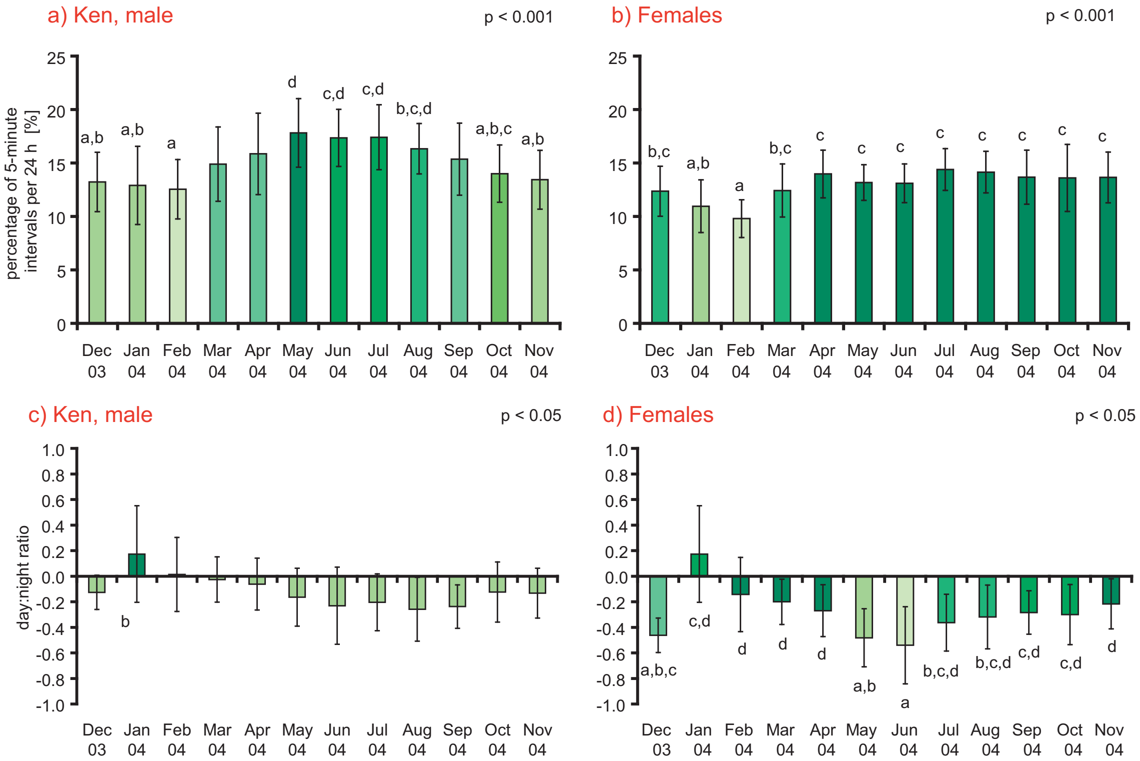

Figure 3.8: Average monthly feeding time and day:night ratio in *Ken* and the females during the year. For details see 3.7. *Ken* showed a clear seasonal pattern in feeding. In May he spent 30% more time feeding than in February, then feeding levels were reduced again. In the females, feeding levels reached a high level in April, but remained high afterwards. With exception of January feeding was always more common during the night. In winter relatively more feeding was observed during the night. This was more pronounced in the females than in *Ken*.

negative values were found in winter, when the mean total time per day spent feeding was higher. This means that the night was the preferred time for feeding. There might also be a correlation between length of night and amount of feeding (Fig. 3.8c). The same pattern was found in the females (Fig. 3.8d).

Locomotion. Locomotion was a behaviour more often observed at night, and showed seasonal variations in chronoethograms (see App. A) and time budget. However, in *Ken* these differences are not significant, probably because of the high standard deviation between single days (Fig. 3.9a). In the females, differences between single months are significant (Fig. 3.9b). The highest levels of locomotor activity have been observed in December and January, the lowest between August and November, when feeding was high and two of the females had joeys leaving the pouch (joeys are not included in the analysis).

The negative day:night ratios underline the patterns in the ethograms. In the male,

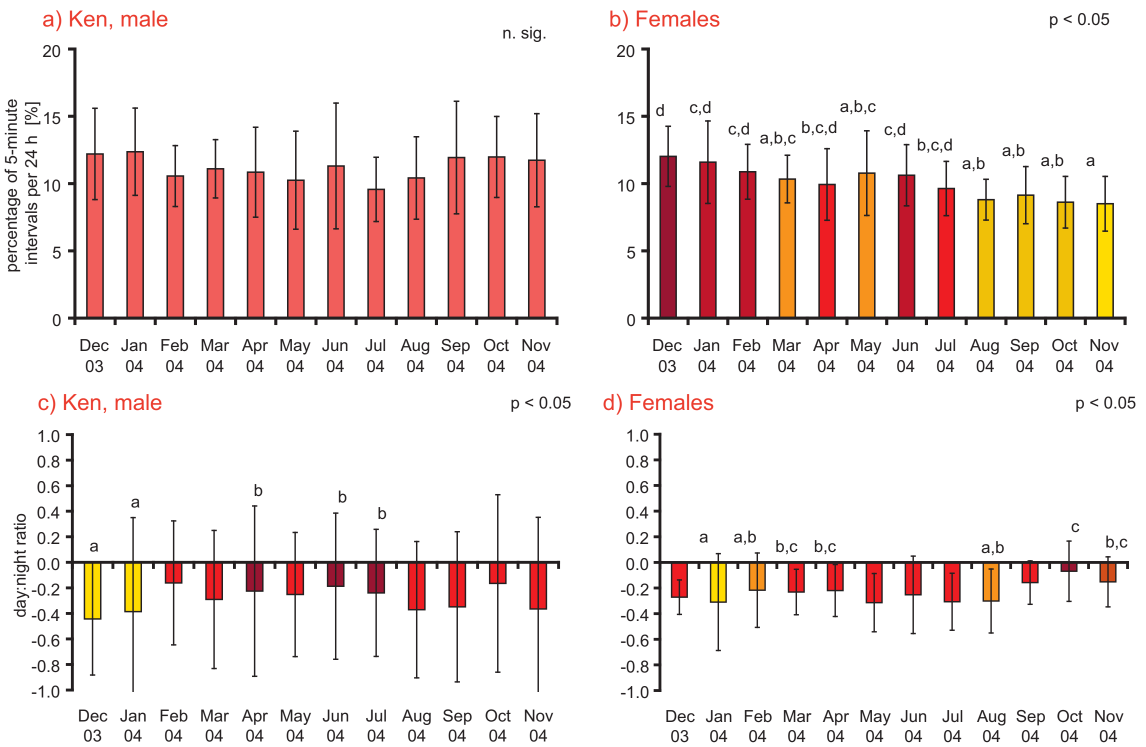

Figure 3.9: Average monthly time of locomotor activity and day:night ratio in *Ken* and the females during the year.
For details see Fig. 3.7. Values in *Ken* varied throughout the year, but these differences were not significant. In the females locomotor activity was more common between December and February and decreased afterwards. In all koalas locomotor activity was more common during the night. The male did not show a seasonal pattern, while the females had a less negative ratio in autumn and spring.

standard deviation between days is high, but there was relatively more locomotor activity during the shorter days in Southern winter than in summer (Fig. 3.9c). In the females locomotor activity was more equally distributed between day and night during autumn and spring, while in summer and in winter it was common at night (Fig. 3.9d). So despite seasonal changes in the females, day:night ratio was not related to day length.

3.1.4 Feeding bouts

Feeding bouts have been the longest activity bouts observed in koalas. The average number of feeding bouts per day did not differ significantly between sexes. On average, 7.2 ± 1.90 bouts per day have been observed in *Ken* and 6.5 ± 2.11 bouts in the females. The duration of a single feeding bout varied greatly, ranging between five and 190 minutes, with an average length of 31.1 min and a median of 25 min. The mean duration of feeding bouts in the females was significantly shorter than in *Ken*. They had slightly more

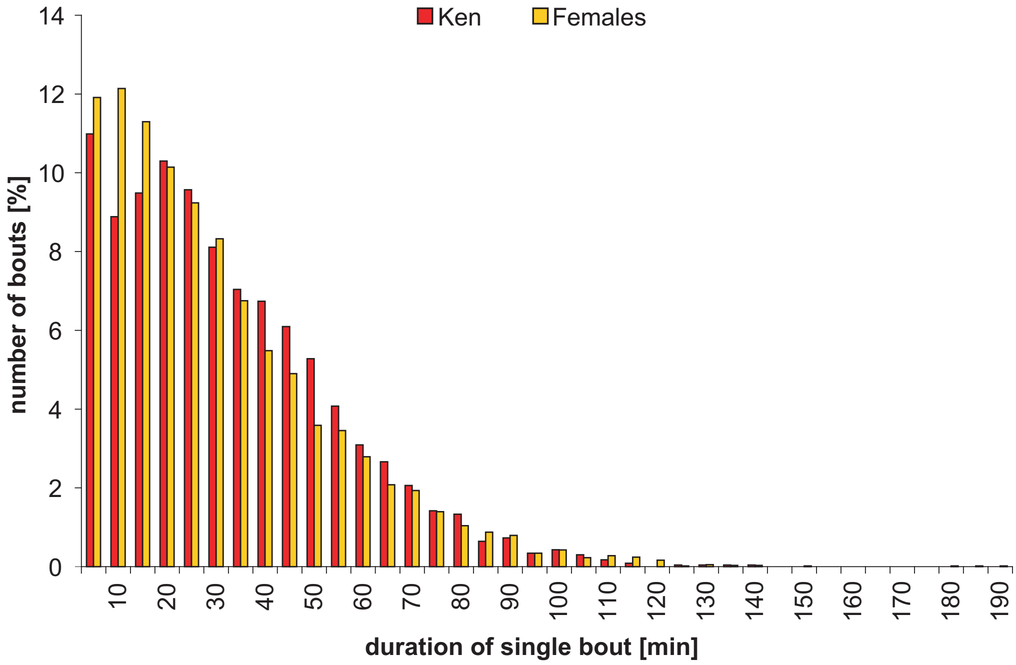

Figure 3.10: Duration of single feeding bouts in *Ken* and the six females.
Histogram calculated of all feeding bouts observed within one year. Number of observed feeding bouts N_{Ken} = 2330, $N_{Females}$ = 6162. In the females short feeding bouts were more common than in *Ken*. His median is 30 min (six intervals), the females' median is 25 min (five intervals). However the longest feeding bouts have been observed in females.

short feeding bouts, but three very long bouts (180, 185 and 190 minutes) have been observed (Fig. 3.10). Bouts longer than 90 minutes were very rare. The longest feeding bouts usually began with the Keeper's Talk.

3.1.5 Reference-Ethograms

For a better comparison with the koalas in two European zoos and for a more detailed analysis of the behavioural categories, exemplary ethograms of one month in winter have been plotted. These ethograms serve as a reference ("reference-ethogram") for the behavioural pattern in a defined condition. A representative example for most of the koalas is *Ken*, the male (Fig. 3.11. An exception from this activity pattern was the female *Yindi*, one of the smallest females (Fig. 3.12). For information on the activity pattern of the remaining females, see Appendix A.

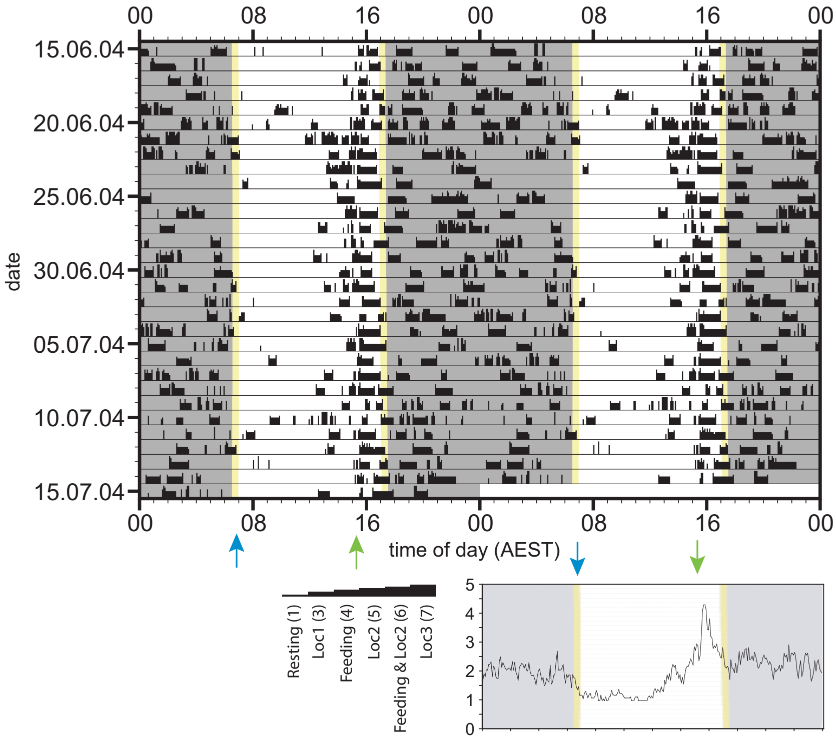

Figure 3.11: Total activity for the male *Ken* in Southern winter.
Upper panel: double-plotted chronoethogram from 15 June to 15 July 2004. Height of the black columns in the ethogram indicates the level of activity. Lower panel: (left) amplitude code of the plotted behaviours, (right) single-plotted activity profile (5 minute intervals) averaged over the complete observation period, same time scale as ethogram above. Background colours: grey = night; yellow = twilight. Blue arrow = morning cleaning, green arrow = Keeper's Talk.

Ken's activity pattern was similar to that of all females except *Yindi* (Fig. 3.12). There was a clear circadian pattern with little activity in the morning,. Activity increased after noon with a small peak before 14:00 and a maximum peak at 16:00, right after the Keeper's Talk. Regular bouts were observed during the night, so the average level of activity at night well above day level.

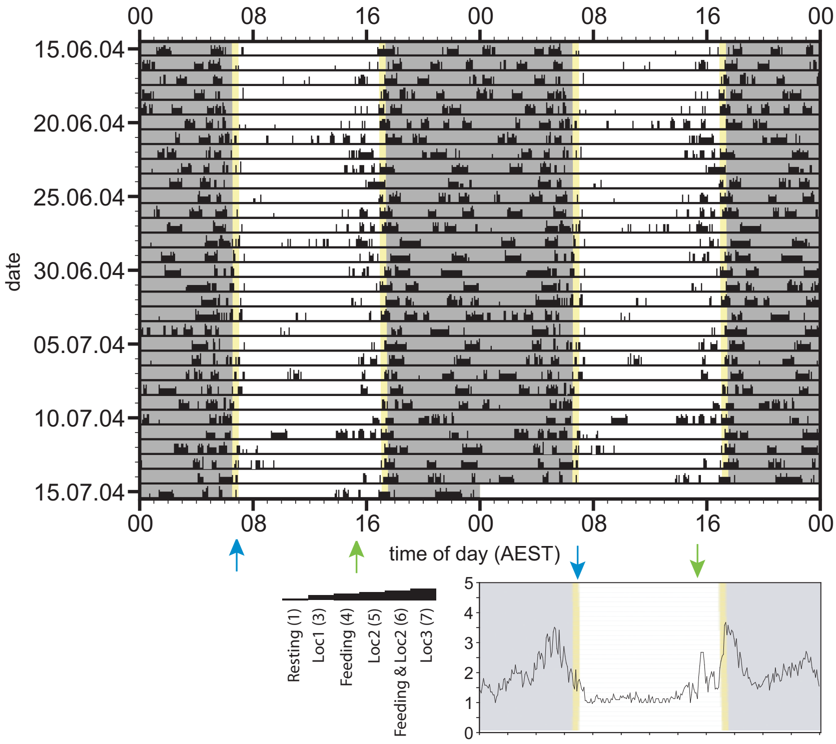

Figure 3.12: Total activity for the female *Yindi* in Southern winter (June - July).
For details see Fig. 3.11. *Yindi*'s chronoethogram showed the strongest relation to twilight compared to the other koalas. Activity was rare during the complete daytime. Peaks of activity were observed at twilight, and there were frequent bouts during the night, keeping the average level of activity well above daytime level. There was only a small activity peak at the Keeper's Talk.

Resting. The koalas rested for most of the 24 hours, so the ethograms and activity profiles for resting (Fig. 3.13) are the mirror image of the diagrams for total activity (Figs 3.11 and 3.12). This becomes obvious when comparing the activity profile of *Ken* (Fig. 3.14). In this chapter, ethograms for resting are shown for both Sydney koalas to give an impression of the pattern (Fig. 3.13). In *Ken* resting was concentrated to the morning and basically ended with the Keeper's Talk. *Yindi* rested during the whole daytime. She showed two regular gaps in resting, one at dusk and one prior to dawn. Resting bouts at night were shorter than during the morning and their duration varied greatly. In *Ken* (Fig. 3.13a), the interruption in resting after the Keeper's Talk was clearly seen, in *Yindi* (Fig. 3.13b) there were two gaps in resting, related to twilight.

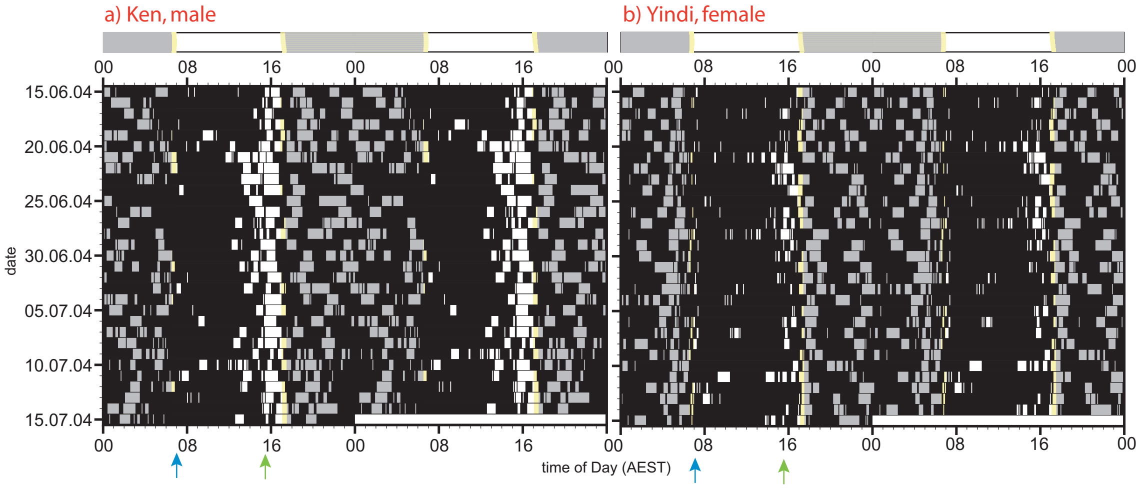

Figure 3.13: Resting for *Ken* (a) and *Yindi* (b) in Southern winter.
Upper panel: double-plotted chronoethogram from 15 June to 15 July 2004. Black bars indicate resting. Bar on top of the graph indicates light-dark regime, grey = night, yellow = twilight, white = day. Lower panel: single-plotted activity profile (5 minute intervals) averaged over the complete observation period, same time scale as ethogram above. Background colours: grey = night, yellow = twilight. Blue arrow = morning cleaning, green arrow = Keeper's Talk.

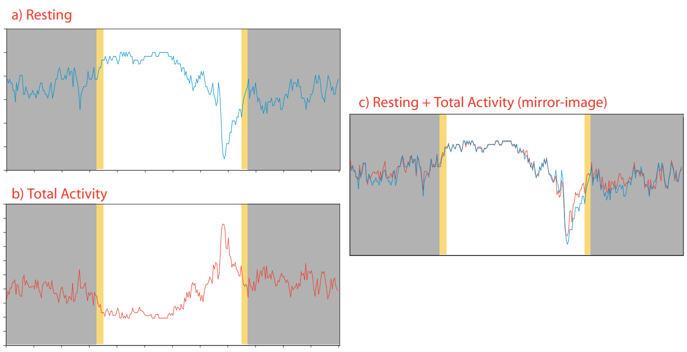

Figure 3.14: Comparison of resting and total activity for *Ken*.
Single-plotted activity profile (5 minute intervals) averaged from 15 June to 15 July. Background colours: grey = night, yellow = twilight. Blue line = resting, red line = locomotor activity. Activity profile for total activity has been mirrored horizontally in (c). Discrepancies between graphs in (c) are due to differences in y-scale. Low resting levels in (a) are reflected by high activity levels in (b). This is especially obvious in the lull in (a) and the peak in (b). The inverted profile for total activity is nearly identical with the profile for resting.

Feeding. Both koalas show a clear day-night discrimination, with little feeding during day time and frequent feeding bouts at night (Fig. 3.15). In *Ken*, there was some feeding in the early afternoon and an obvious feeding peak at 15:30. After the keeper had provided fresh browse at the beginning of the Keeper's Talk, *Ken* usually started to feed within 20 minutes. This peak was also seen in most of the females. Usually two or more females fed

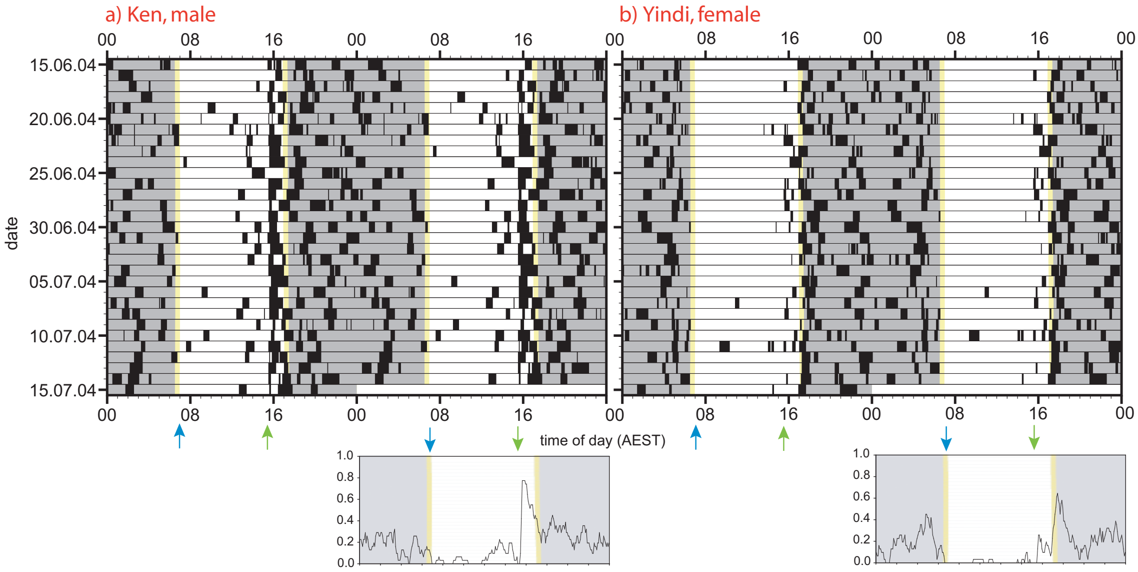

Figure 3.15: Feeding for *Ken* (a) and *Yindi* (b) in Southern winter.
Black bars indicate feeding. For further details see Fig. 3.13.
Both koalas showed a clear day-night pattern with more feeding at night. In *Ken*, there was a feeding peak after the Keeper's Talk. In *Yindi* a similar peak was observed at dusk. She almost exclusively fed during the night. Feeding in both koalas ceased with dawn.

during the Keeper's Talk. This bout was one of the longest observed during the day. For the remaining afternoon as well as for the first part of the night, several bouts of medium lengths followed. Feeding bouts became less frequent after midnight. This pattern was also seen in most of the females, but *Ken* fed significantly longer than the females' average (Fig. 3.5).

Yindi fed almost exclusively during the night. She did not react as strongly to the Keeper's Talk as the other koalas, but showed a feeding peak at dusk (Fig. 3.15b). The ethogram shows a band around dusk and basically two bands during the night, one before midnight and a second one around 04:00 and 05:00 in the morning. Feeding ceased right before dawn.

Locomotion. Due to the length of an interval, locomotor activity has been classified into three levels. Loc1 (short change of place) was rare in all koalas and usually occurred in isolated single bouts. Loc2 was the most common level of locomotor activity observed at Koala Walkabout for changing location and often took place in connection with feeding. Loc3 (locomotor activity for more than three minutes, including wandering and intensive climbing/jumping) was not as common as Loc2 and was not observed on all days. It was rare during the day.

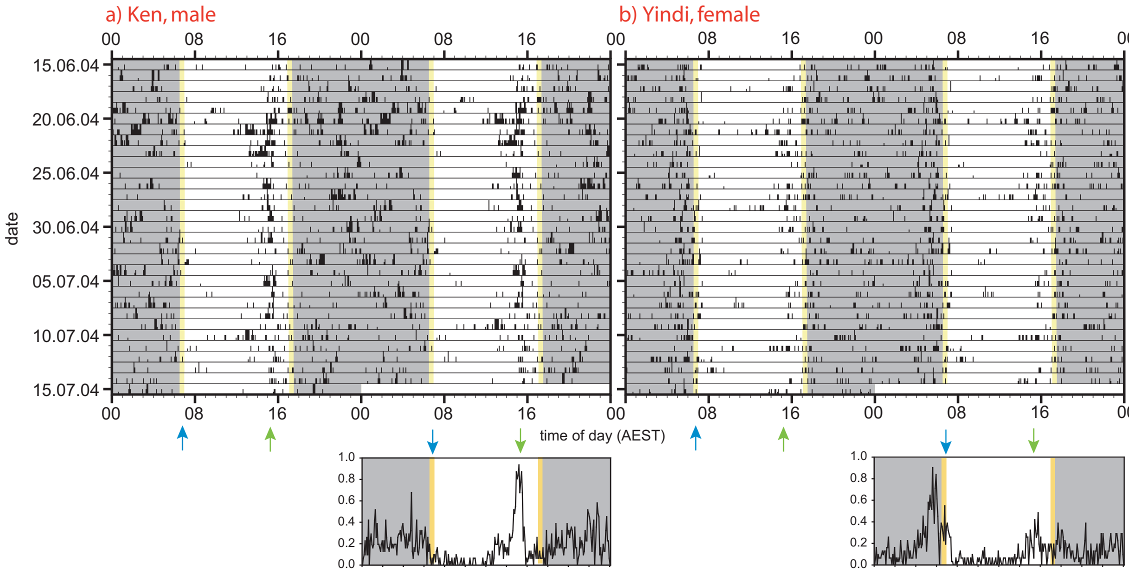

Figure 3.16: Locomotor activity for *Ken* (a) and *Yindi* (b) in Southern winter.
Height of column indicates level of locomotor activity (Loc1, Loc2 and Loc3). For further details see Fig. 3.13. In *Ken* there was a clear band of locomotor activity right before and at the beginning of the Keeper's Talk. Locomotion stayed frequent for the remaining afternoon and night, ceasing at sunrise. In *Yindi* locomotor activity was mostly observed during the night with a concentration in the last hours of the night. There also was a concentration around Keeper's Talk.

In *Ken*, as in most of the females, there was a clear concentration of locomotor activity prior to the Keeper's Talk (Fig. 3.16a). Its onset differed between days, starting up to three hours before the keeper entered. During the night, locomotor activity was frequent. Often it was observed in only one interval, but in some nights there were longer bouts of locomotor activity. Locomotion in *Ken* ceased with sunrise and was rarely seen during the morning.

In *Yindi* the difference between day and night was more pronounced (Fig. 3.16b). The peak prior to Keeper's Talk was weak and only slightly higher than that after dusk. On some days *Yindi* moved around frequently until the beginning of the night. Short locomotion bouts can be seen during the night. In the last hours before sunrise, locomotor activity became more frequent, although no clear band was visible. It stopped with sunrise.

Although the basic pattern did not change during the observation period, there were changes in intensity of locomotor activity at certain times. There have been several days, were longer bouts of locomotor activity have been observed, especially between 18 and 23 June. During this time he has been observed on the ground more frequently than usually. In the female *Carrie*, there has been slightly more locomotor activity at the same time, but not in *Yindi*. No data are available to explain this.

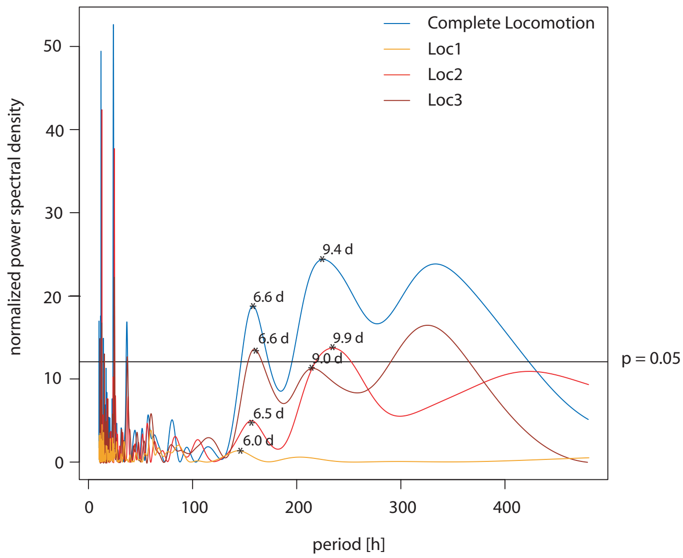

Figure 3.17: Power spectrum of locomotor activity for *Ken* calculated over the observation period of 30 days.

Power spectrum calculated from 15 June to 16 July 2004 (winter) for complete locomotor activity and locomotion levels 1-3. Peaks above horizontal line indicates significant period length (p=0.05).

Locomotor activity showed two significant ultradian periods. The first one of 6.6 days was significant for complete locomotion and Loc3. The second peak of about 9.4 days was significant for complete locomotor activity and Loc2.

Ken does also not show intense locomotor activity at the Keeper's Talk every day. Instead there are regular gaps in the band at 15:30. These gaps are not related to the weekend or other days of the week. However, the power spectrum shows significant period lengths of 157.9 hours (6.6. days) and 225.5 hours (9.4 days)(Fig. 3.17). Similar period lengths were calculated for each of the three levels of locomotor activity (Loc1-3). These data suggest an endogenous rhythm, not an externally triggered reaction. *Carrie* and *Yindi* do not show a similar pattern.

On ground. *Ken* was regularly seen on the ground, but rarely in the morning. A clear band is visible prior and during the Keeper's Talk (Fig. 3.18b). Several bouts followed during the night. *Yindi* was hardly ever on the ground during the day and did not display a peak at the Keeper's Talk. Her profile shows a peak in the last hour of the night (Fig. 3.18b).

Koalas usually came to the ground briefly mainly to change trees or walk to the entrance door. Only *Ken* sometimes stayed on the ground for a longer period of time, exploring different trees and the scrubs. At the beginning of the Keeper's Talk, the keeper put

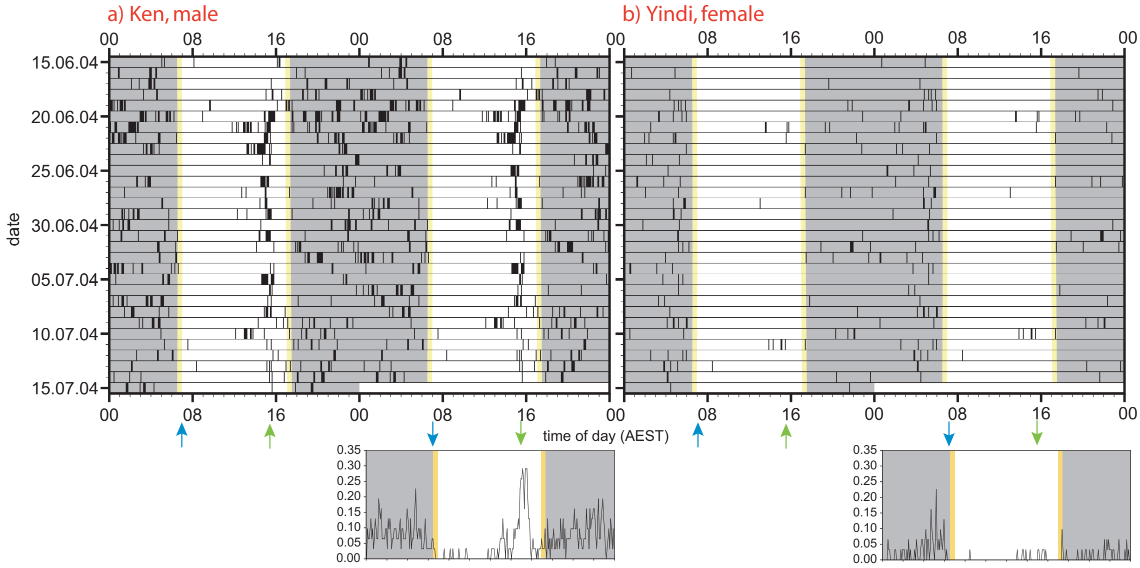

Figure 3.18: Presence on the ground for *Ken* (a) and *Yindi* (b) in Southern winter.
Black bars indicate presence on ground. For further details see Fig. 3.13.
The koalas were more often on the ground at night. *Ken* also showed a high peak prior to the Keeper's Talk. *Yindi* was hardly ever on the ground during daytime. She came to the ground most often in the last two hours of the night.

fresh browse on the ground to divide the branches for the different vases. In rare occasions *Ken* or *Adori* actually fed from the browse on the ground. There was one extraordinarily long resting period on 13 October, when *Ken* sat in the shade of the Pittosporum tree for 3 hours and 50 minutes (see Fig. A.12). This was the hottest day of the summer, reaching its maximum temperature of 38.2°C at around 16:00. At 15:00 keepers sprayed the enclosure with water.

3.2 Duisburg

3.2.1 Chronoethogram and activity profiles

The four koalas observed at Duisburg Zoo showed individual activity pattern. Therefore all patterns will be shown in the following. There has been a data gaps from 13 June, 21:35 to 16 June 08:00.

Total activity. In *Kambara*, there was no obvious difference in the distribution of activity bouts between day and night (Fig. 3.19). In summer activity increased after 19:00 and remained on this level until the end of natural dusk. At night few, usually short activity periods could be seen. There was a small peak at the beginning of natural dawn, then activity decreased. In winter activity levels increased during natural dusk and remained on a high level from 16:00 to 20:00. Afterwards activity bouts during the night were few and mean activity levels were not much higher than during day. In both sesaons there was a high activity peak in the morning, in summer at 10:00, in winter from 09:00 to 11:00. On days with weighing the behaviour was not noticeably different from other days (Fig. fig:DUI-weighing).

There was a distinct circadian pattern with very little activity during the day in *Yuri* (Fig. 3.20). In summer, activity slowly increased after 19:00, peaked shortly before the artificial lights were turned off and ended after natural dusk. On most days in winter activity started between sunset and the end of the artificial day. A peak is visible when the lights were turned off. Several activity bouts followed during the night. In summer, activity ceased with natural sunrise. In winter, there was an activity peak between 05:00 and 06:00 before activity ceased at 07:00, shortly before natural dawn respectively the turning on of the lights, which was at about the same time. In summer, a small peak was visible between 08:00 and 09:00. The weighing was usually followed by one interval of locomotor activity, resulting in a small peak. In winter there was no regular activity during the day. During both seasons, independent from weighing, *Yuri* rested around 11:00.

In *Kangulandai* activity was distributed throughout the complete 24 hours without an distinct pattern. In summer there were some differences between day and night (Fig. 3.21 top). *Kangulandai* was active throughout the complete day, but activity was lower during the day with exception of a peak between 10:00 and 13:00. From 29 June to 08 July a second band was visible in the afternoon. At night there was a peak when the lights were

Legend for Figures 3.19 to 3.22.: Double-plotted chronoethograms and activity profiles from 3 June 2003 to 14 July 2003 (top) and 8 November to 20 December (bottom). Upper panel: chronoethogram, height of black columns indicates level of activity. Lower panel: (left) amplitude code of the plotted behaviours, (right) single-plotted activity profile (5 minute intervals) averaged over the complete observation period, same time scale as ethogram above. Background colours: dark grey = night, light grey = artificially extended day, yellow = twilight, vertical orange line = lights on / off. Blue arrow = morning cleaning and feeding (no exact time), vertical red arrow = time of weighing (not daily), horizontal red arrow = time of weighing.

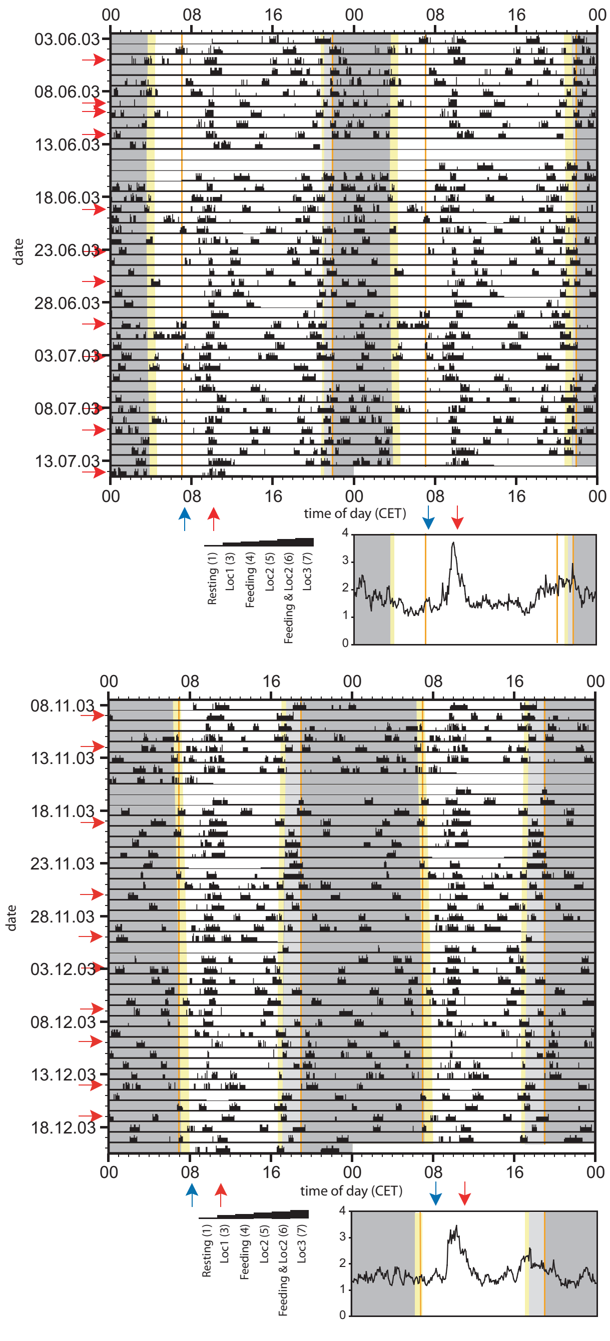

Figure 3.19: Total activity for the male *Kambara* in Northern summer and Northern winter.
For details see page 3.2.1.

In *Kambara*, there is no strong discrimination between day and night, activity bouts are distributed over the complete 24 hours. In summer, activity increased around 17:00 and dropped again after natural sunset. In winter, extended activity periods have also been observed during twilight. In summer, there is an activity peak at 10:00. In winter this peak is broader and last from about 09:00 to 11:00. Little activity was observed during the night and between the peaks.

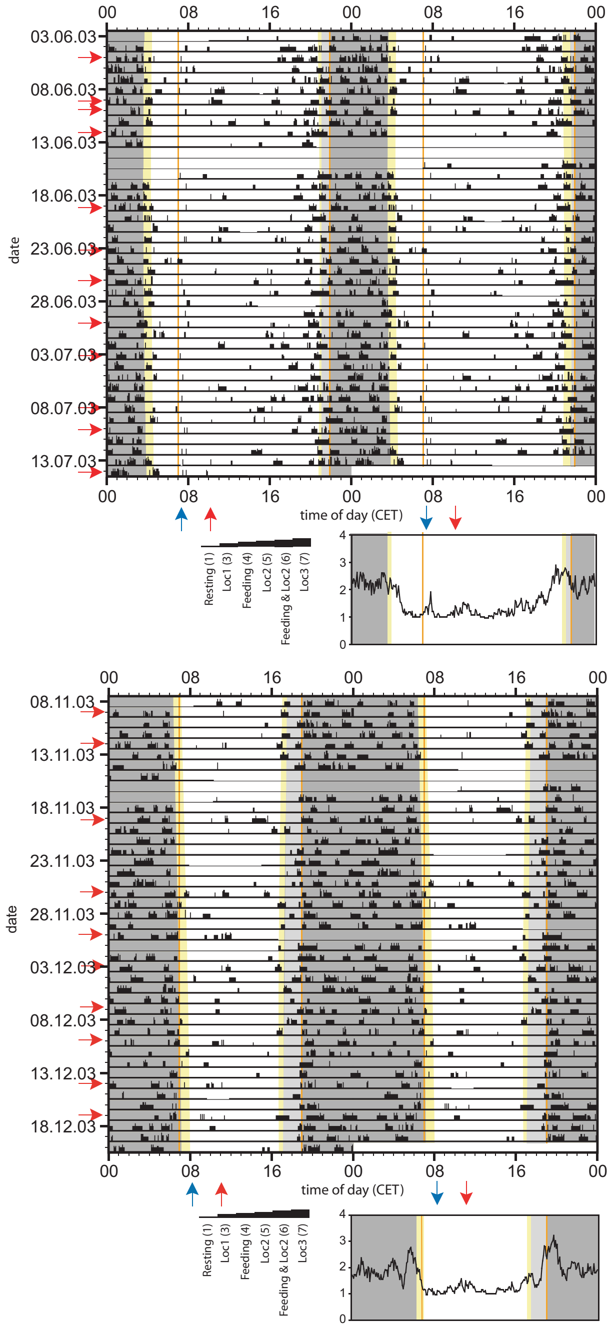

Figure 3.20: Total activity for the female *Yuri* in Northern summer (top) and winter (bottom).
For details see page 3.2.1.
There was a clear discrimination between day and night with almost no activity during the day. In summer activity increased about two hours prior to natural dusk, peaked shortly before the lights were turned off and ended after natural dusk. In winter, *Yuri* displayed an activity peak right after the beginning of the artificial night. Nocturnal activity in summer was higher than in winter, but shorter. In summer, a weak activity peak was visible during the morning cleaning.

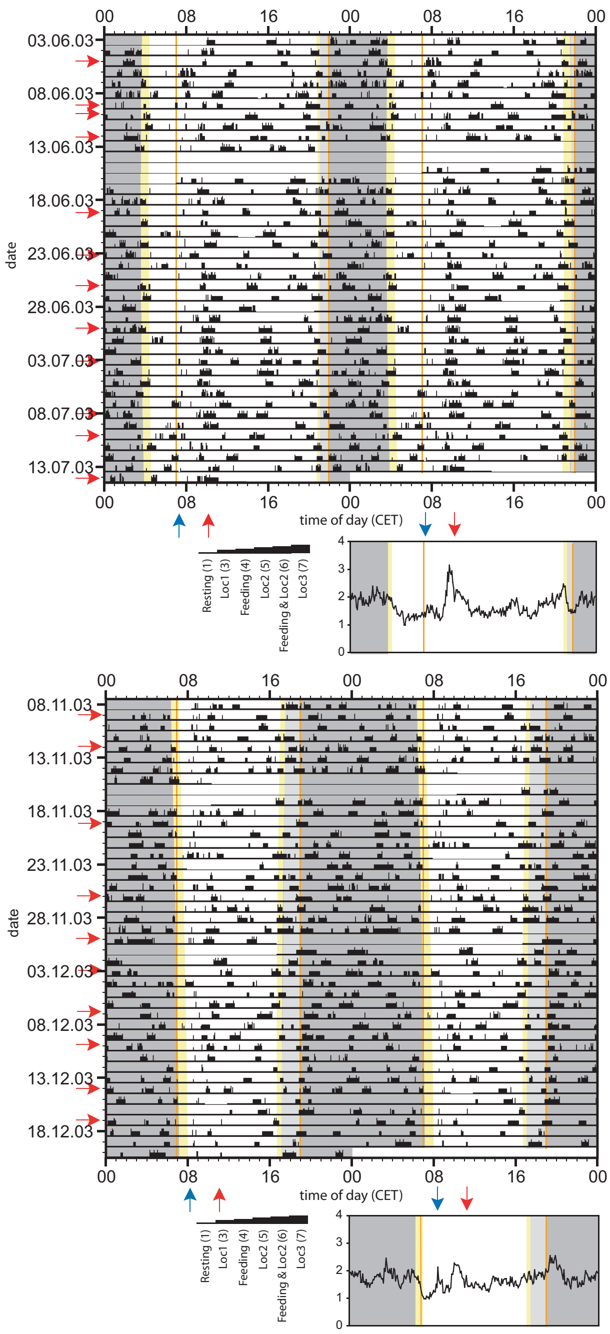

Figure 3.21: Total activity for the female *Kangulandai* in Northern summer (top) and winter (bottom). For details see page 3.2.1.

In summer, activity was lower during the day with exception of a peak between 09:00 and 12:00. In winter, there was no distinct pattern. At 07:00 there was a lull, followed by peaks at 08:00 and 10:00. There also was a small increase in activity at the beginning of the night. Activity during the day was only slightly lower than during the night.

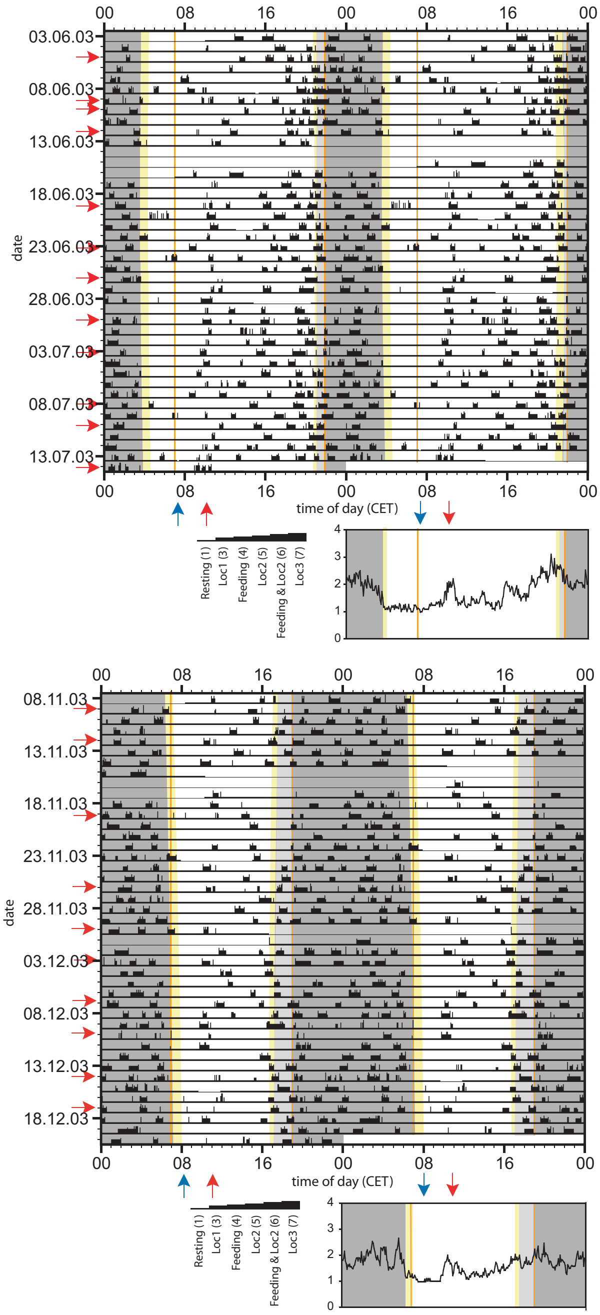

Figure 3.22: Total activity for the female *Allora* in Northern summer (top) and winter (bottom).
For details see page 3.2.1.
There was a clear day-night pattern with more activity during the day. Activity was lowest in the morning and there was a low, but broad peak between 09:00 and 10:00 in winter, which was mostly feeding.

switched off and shortly after sunset, followed by a short lull. During the remaining night frequent activity bouts followed until activity was reduced between natural sunrise and the switch-on of the lights. In winter,no clear pattern was visible (Fig. 3.21 bottom). There was a lull at 07:00 and two peaks in the morning, one at 08:00, the time the keeper usually started his morning work in the enclosure and at 10:00, which was mainly feeding. A small increase in activity was seen at the beginning of the night. In both seasons there was no noticeable difference between days with and without weighing (Fig. 3.54).

Allora had a clear day-night pattern, which did not differ distinctly between seasons (Fig. 3.22). In summer afternoon activity was higher than in winter. There was a peak at 16:00 and a high peak at natural sunset (ca. 20:00). In winter there was no clear onset of activity, but after 24 November there was a band during twilight and a second band, better visible as peak in the activity profile after the lights have been switched off. Activity was on a high level, especially in summer, until natural sunrise, when it fell on its lowest level. Around 10:00 *Allora* was active on many days in winter. In summer a similar, but smaller peak was seen at 11:00. It was smaller than in winter. Aside of this activity was low during the day, increasing slowly during the afternoon.

Resting. As already demonstrated for Koala Walkabout, resting was observed during most of the day. Ethograms and activity profiles are a mirror image of total activity. Therefore, the pattern of this behaviour will not be described.

Feeding. Feeding was the main activity in all koalas at Duisburg, but again the individual patterns were different and reflected the pattern in total activity.

Kambara had one distinct band in feeding around 11:00 in summer (Fig. 3.24a). Few feeding bouts followed during the afternoon. Feeding increased around 20:00, reaching a peak when the lights were switched off at 22:00 and a second one around 23:00. During the night feeding bouts were slightly more frequent than during the day. In winter, the band in the morning was broader than in winter (Fig. 3.23a). Several feeding bouts followed during the remaining day. During dusk feeding increased. The broad peak appeared with the beginning of natural dusk and ended shortly after the lights were switched off. During the night, feeding bouts were less frequent than during the day. The period with the lowest level of feeding in both seasons was between 8:00 and 9:00, when often no food was available (Fig. 3.25a).

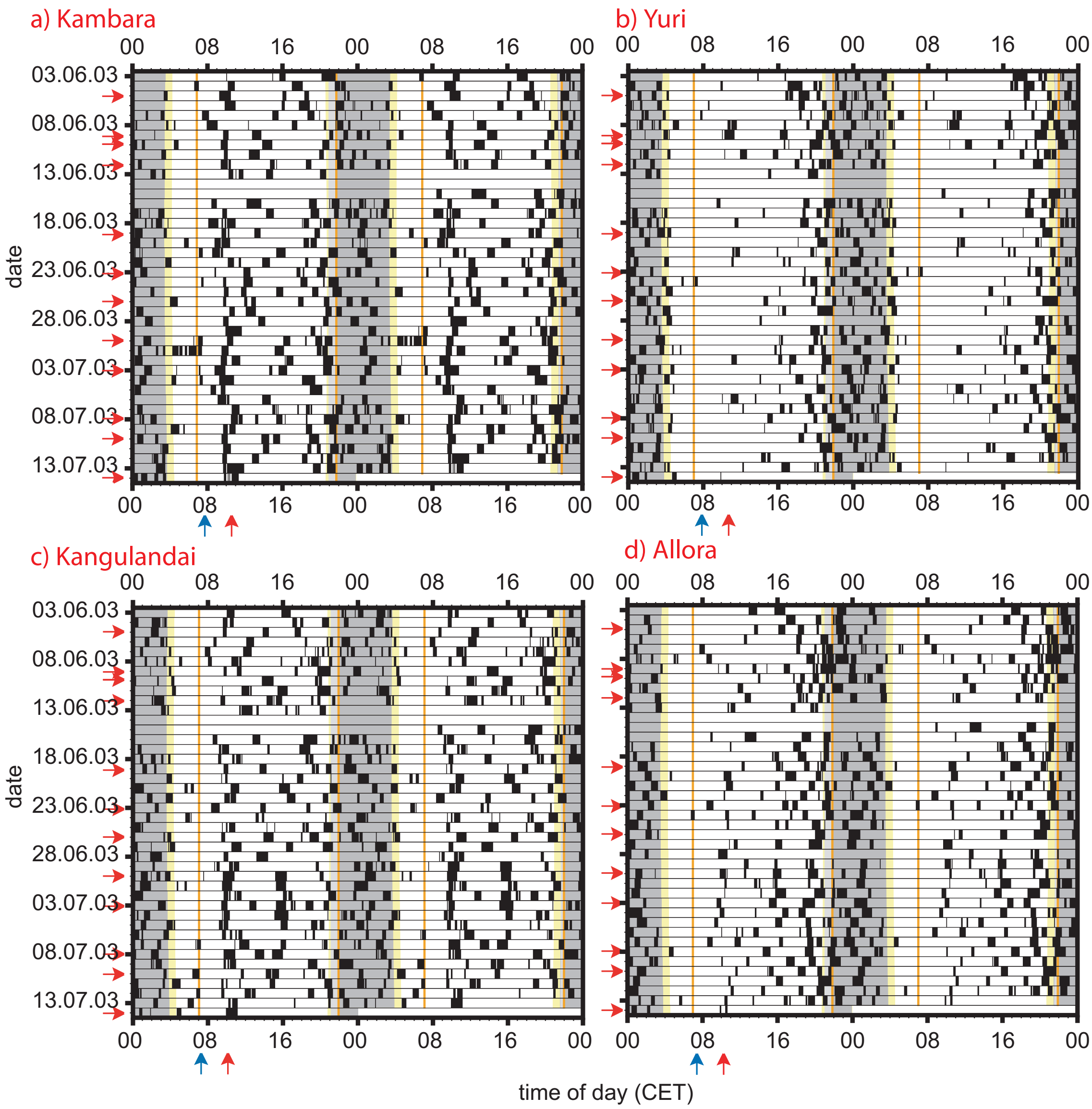

Figure 3.23: Feeding for all Duisburg koalas in Northern summer.

Double-plotted chronoethograms from 3 June to 14 July 2003. Black bars indicate resting. Background colours: dark grey = night, light grey = artificially extended day, yellow = twilight, vertical orange line= lights on / off. Blue arrow = morning cleaning and feeding (no exact time), vertical red arrow = time of weighing (not daily), horizontal red arrow = time of weighing.

In *Kambara* (a) there was a clear band of feeding in the morning and a concentration of feeding during dusk. *Yuri* (b) mostly fed during the night and only on some days during the morning. In *Kangulandai* (c) no distinct pattern was visible. *Allora* (d) had a clear day-night pattern with more feeding during the night.

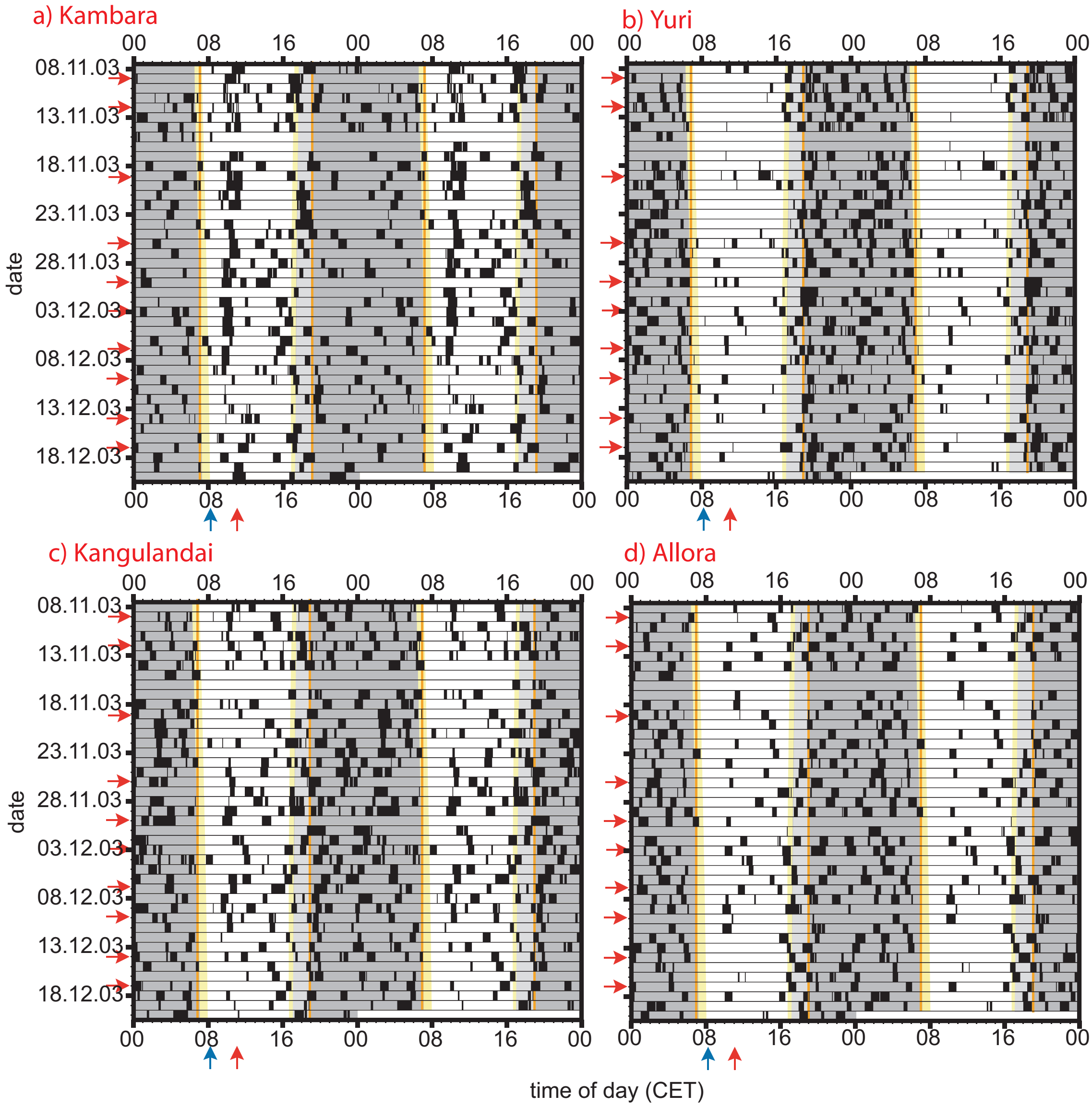

Figure 3.24: Feeding for all Duisburg koalas in Northern winter.
Double-plotted chronoethograms from 8 November to 20 December 2003. For further details see Fig. 3.23. In *Kambara* (a) there was a clear feeding band in the late morning and a concentration of feeding during the evening and night. *Yuri* (b) again showed a clear day-night pattern with feeding being concentrated on the afternoon and the shorter night. *Kangulandai* (c) showed a similar band to *Kambara*, some feeding in the afternoon and concentrated feeding during the night, ending in the morning. In *Allora* (d) feeding again began in the afternoon and was concentrated to the night.

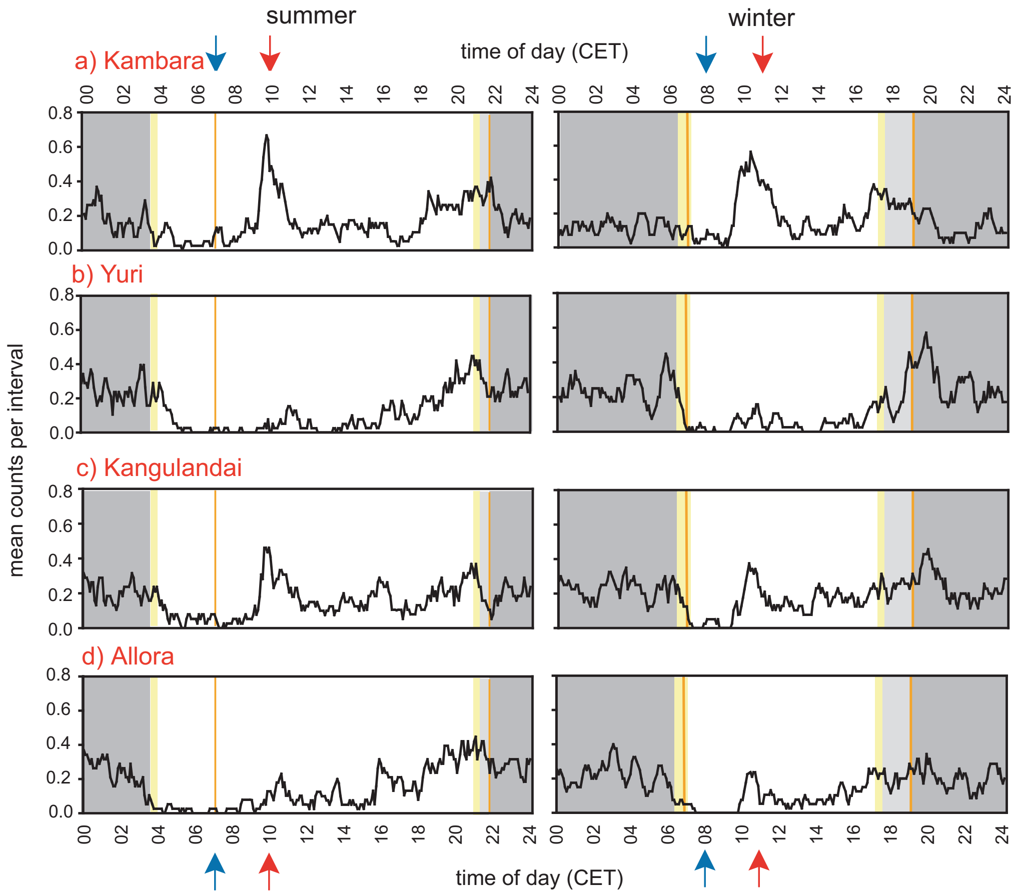

Figure 3.25: Average levels of feeding for all Duisburg koalas in Northern summer and Northern winter. Activity profile (5 minute intervals) averaged from 3 June to 14 July 2003 and from 8 November to 20 December 2003. Background colours: dark grey = night, light grey = artificially extended day, yellow = twilight, vertical orange line = lights on / off. Blue arrow = morning cleaning and feeding (no exact time), red arrow = weighing (not daily).

Clear day-night discriminations were observed in *Yuri* (b) and *Allora* (d), in *Kambara* (a) and *Kangulandai* (c) feeding was more equally distributed over the 24 hours. *Kambara* (a) had a distinct peak of feeding between 10:00 and 12:00 in both seasons. In summer feeding levels were higher during the night. *Yuri* (b) did not show much feeding during daytime. In *Kangulandai* (c), there was little feeding during the morning, but a peak at 10:00 and several irregular peaks during the remaining time. *Allora* (d) fed little during the morning and somewhat during the afternoon, but most feeding was seen during the night and, in winter, in the afternoon.

Yuri showed the same distinct day-night pattern as in total activity and resting. On some days in summer, feeding was seen around 11:00 and there was usually a bout in the afternoon, but generally there was little feeding during the day (Fig. 3.24b). Feeding started to increase after 17:00 with a peak during dusk and the highest peak after sunset (Fig. 3.25b). Feeding bouts were frequent during the night, reaching another peak between 05:00 and 06:00 during natural dawn. Feeding ceased after natural sunrise. In winter, feeding bouts could be seen between 09:00 and 12:00 (Fig. 3.23b). Feeding increased during natural dusk and reached the highest peak of the day one hour after the lights were switched off, at 20:00. During the nights several feeding bouts followed and a second peak was visible at 06:00. After the lights were switched on, no feeding was observed until fresh browse had been provided.

Kangulandai had a similar pattern in winter and summer. She did not feed between 07:00 and 09:00 (Figs 3.23c and 3.24c). Then a first peak appeared around 10:00 (Fig. 3.25c). There were some feeding bouts during the day, becoming more frequent in the afternoon and dusk. A second, higher peak appeared in the first hours of the night. Feeding bouts followed throughout the remaining night, and feeding levels were slightly higher than during the day.

In summer, *Allora* had a distinct day-night pattern in both seasons (Figs 3.24d and 3.23d). Feeding was more common during the night. In winter, feeding began after natural sunset or after the lights had been switched off (Fig. 3.23d). In summer, feeding bouts were already common in the afternoon (Fig. 3.24d). Feeding ended with dawn in summer and before the lights were switched on again in winter.

Locomotion. In *Kambara*, there was no obvious day-night pattern in winter (Fig. 3.27a), but in summer locomotor activity was more concentrated on the short night (Fig. 3.26a). In both seasons there was a broad band of locomotion bouts visible in the late morning (winter) respectively around noon (summer). At this time the keeper usually fed fresh browse. A similar band was visible for feeding (Fig. 3.23a, Fig. 3.24b). The activity profile showed only a slight increase at night in winter, but a higher one for the shorter summer nights (Fig. 3.28a).

Yuri showed a very distinct day-night pattern with more locomotor activity during the night (Fig. 3.27b). In summer, locomotor activity was extended into the morning until the lights were switched on (Fig. 3.26b). There was a weak line of locomotor activity in the morning, usually lasting only one or two intervals. At this time the keeper usually started

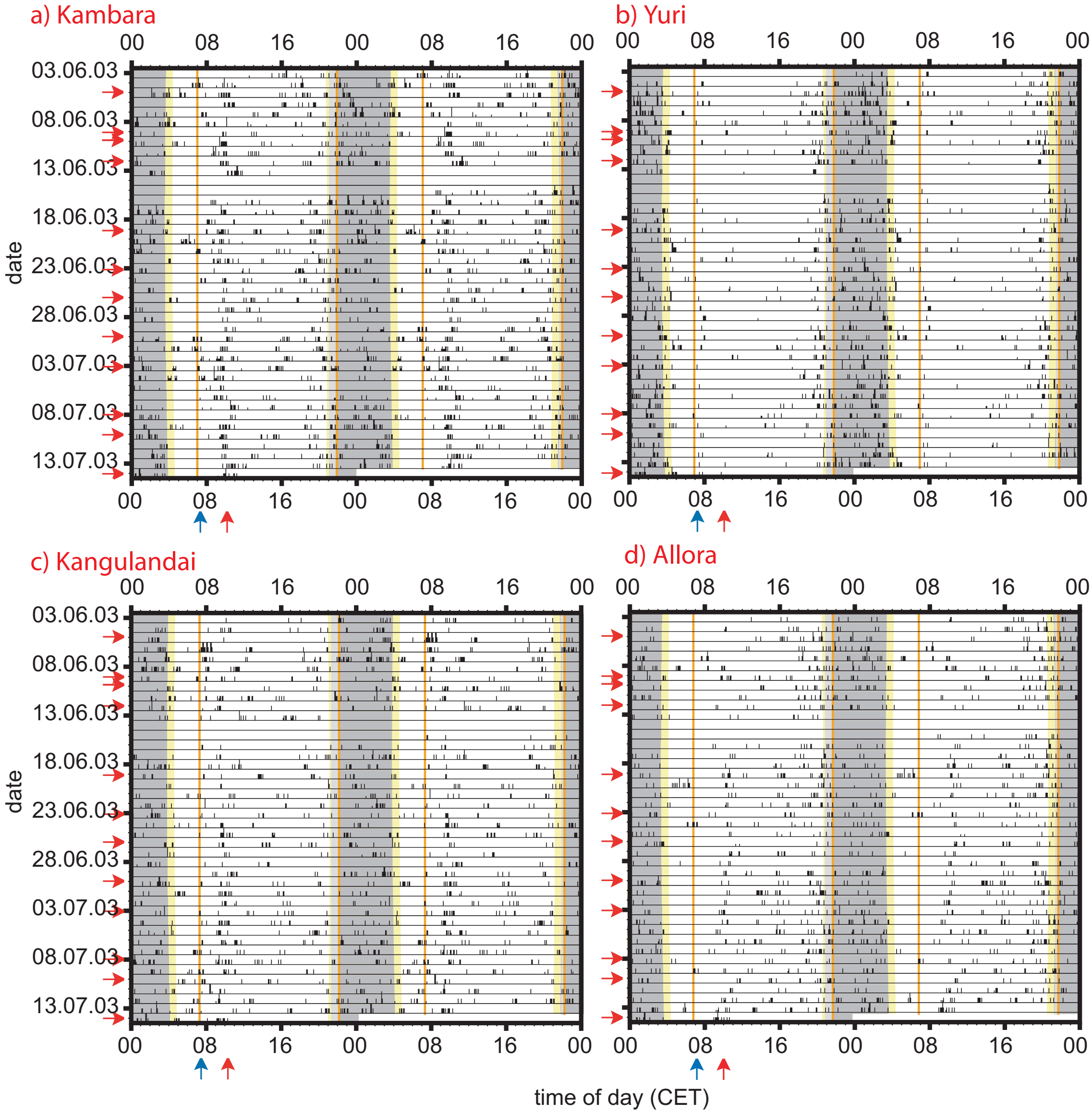

Figure 3.26: Locomotion for all Duisburg koalas in Northern summer.
Double-plotted chronoethograms from 03 June to 14 July 2003. Height of the black columns indicates level of locomotor activity (Loc1, Loc2, Loc3). For further details see Fig. 3.23.
Kambara, (a) displayed a broad band around noon and less locomotor activity during the remaining daytime. At night locomotor activity was more frequent. In *Yuri* (b) locomotor activity was concentrated to the night and the morning before the lights were switched on. A band was visible in the morning, but locomotor activity was rare in the remaining day. In *Kangulandai* (c) locomotor activity was scattered over the day with a band in late morning. *Allora* (d) did rarely show locomotor activity in the morning, but a band around noon and scattered bouts in the afternoon and night.

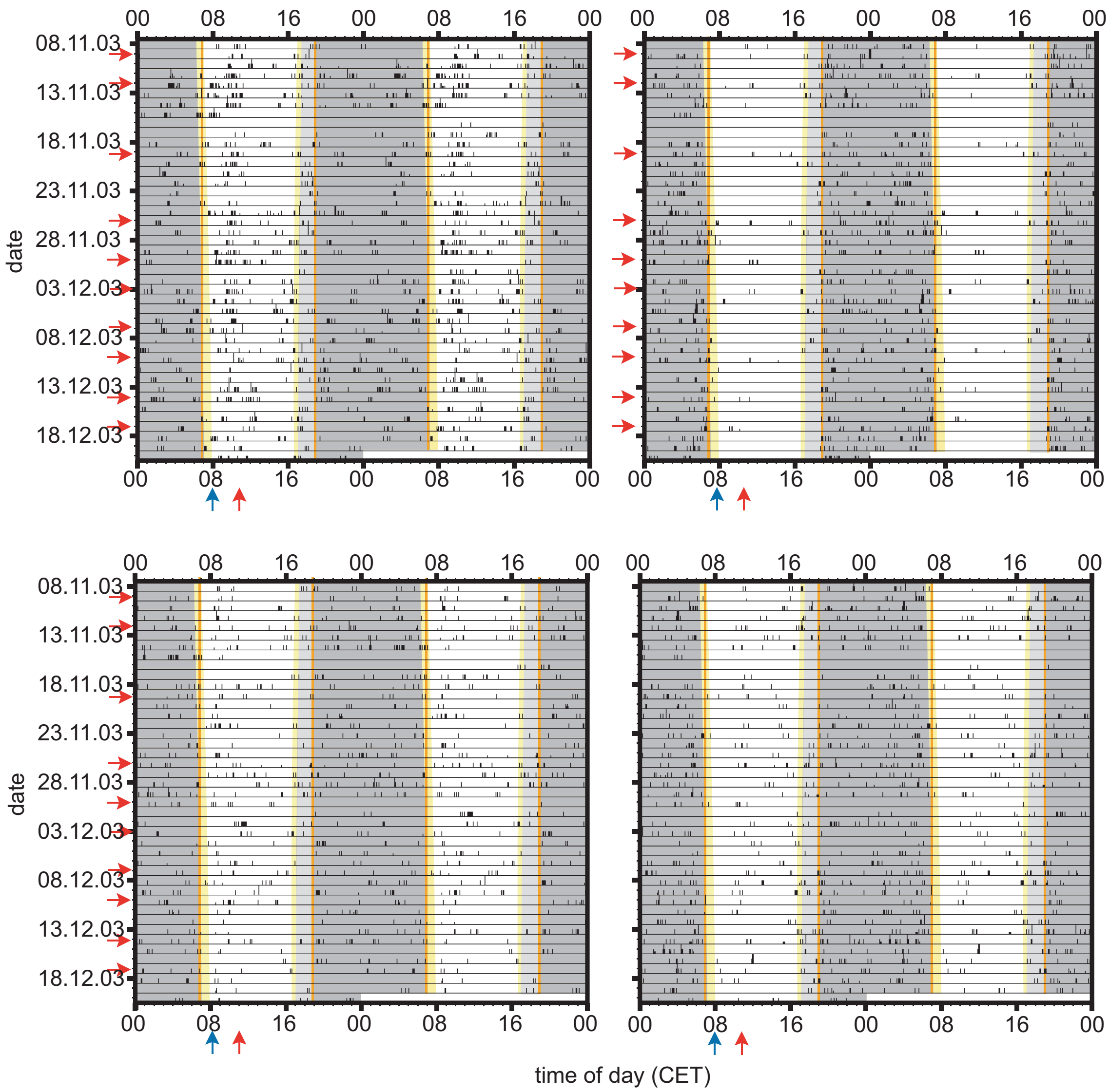

Figure 3.27: Locomotion for all Duisburg koalas in Northern winter.
Double-plotted chronoethograms from 08 November to 20 December 2003. Height of the black columns indicates level of locomotor activity (Loc1, Loc2, Loc3). For further details see Fig. 3.23.
Kambara (a) showed a broad band of locomotor activity in the morning and a weaker one during dusk. Locomotion bouts in between were of different length. *Yuri* (b) showed locomotor activity almost exclusively during the night with a band around 11:00. *Kangulandai* (c) also showed no obvious pattern, but less locomotor activity during the afternoon. In *Allora* (d) locomotor activity was more common during the night with few bouts during the day.

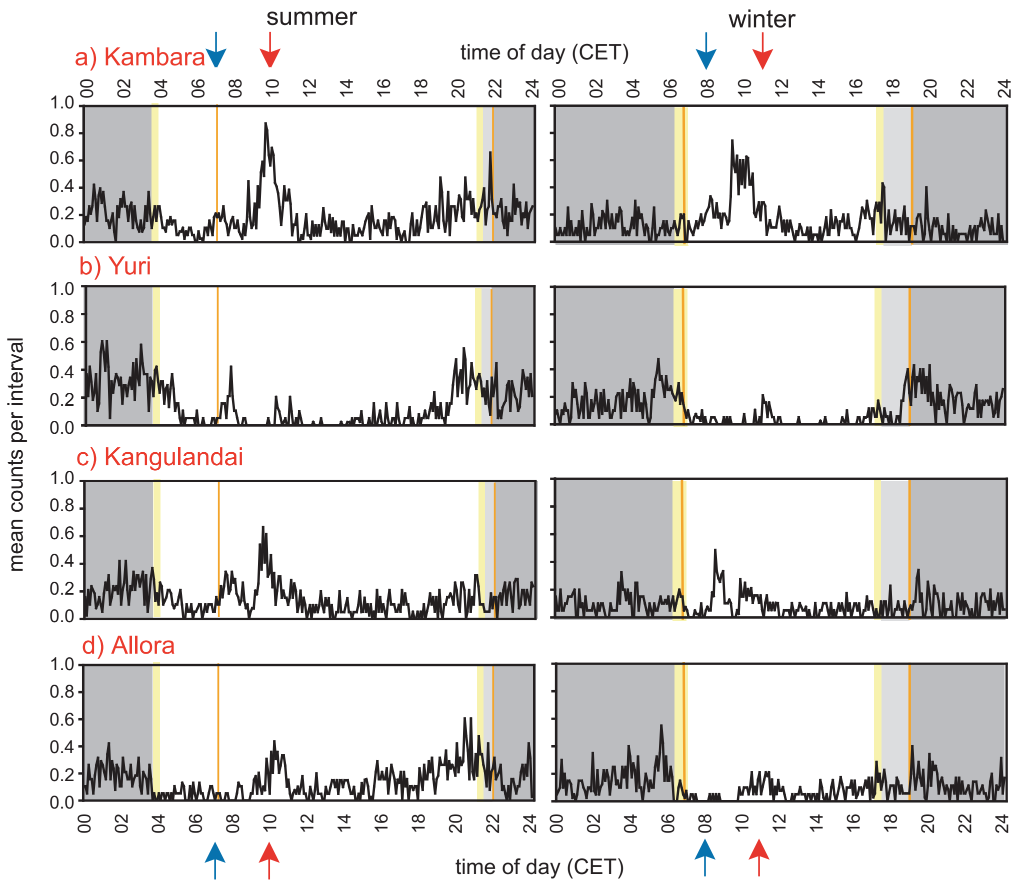

Figure 3.28: Average levels of locomotor activity for all Duisburg koalas in Northern winter and Northern summer.

For details see Fig. 3.25

Kambara (a) showed only slightly more locomotor activity at night, but a clear peak around 10:00, which is broader in winter. In *Yuri* (b) locomotor activity was rare during daytime; in summer it was extended into the morning. In *Kangulandai* (c) locomotor activity was higher at night in summer, but not in winter. There were two peaks in the morning and around noon. In *Allora*,(d) locomotor activity was more frequent during the night, but there was a small peak around noon.

to work in the enclosure. The discrimination between day and night was also visible in the activity profiles. In winter locomotor activity during most of the day was almost zero (Fig. 3.28b).

Kangulandai also lacked a clear pattern, but in summer there was a concentration between 11:00 and 12:00 (Fig. 3.27c, Fig. 3.26c). The activity profiles also showed no strong differences between day and night, though there was slightly more locomotor activity during the night in winter (Fig. 3.28c).

In *Allora*,there was slightly more locomotor activity during the night in winter, but it was slightly prolonged into the day (Fig. 3.27d). There was almost no locomotor activity in the morning, but a slight concentration in the late morning at the same time as in the other koalas. In summer the band between 11:00 and 12:00 was clearer (Fig. 3.26d). During the afternoon, frequent locomotor activity has been. It increased towards evening. The activity profile showed that locomotor activity in summer reached a higher level shortly before dusk and was extended into the early morning (Fig. 3.28d). In winter locomotor activity was more concentrated to the night.

On ground. Generally the koalas spent little time on the ground. Therefore levels in the activity profile were very low and peaks originated from few events (Fig. 3.31). *Kambara* showed no distinct day-night pattern, but there were two peaks in the morning, in winter a higher one at 08:00 and a smaller one at 10:00 (Fig. 3.30a), in summer around 05:00 and at 09:00 (Fig. 3.29a). *Kambara* was regularly on the ground between these peaks. *Yuri* was mostly on the ground after midnight in summer (Fig. 3.31b), but she also came to the ground in the early morning, which was in accordance with her locomotion pattern (Fig. 3.26b). She was not seen on the ground during the day in winter (Fig. 3.29b). In winter *Kangulandai* was seen on the ground only on few days and than exclusively during the night (Fig. 3.30c). In summer she came down more frequently and now also in the early morning (Fig. 3.29c). *Allora* was observed only once on the ground during daytime in winter and also rarely in summer (Fig. 3.30d, Fig. 3.29d).

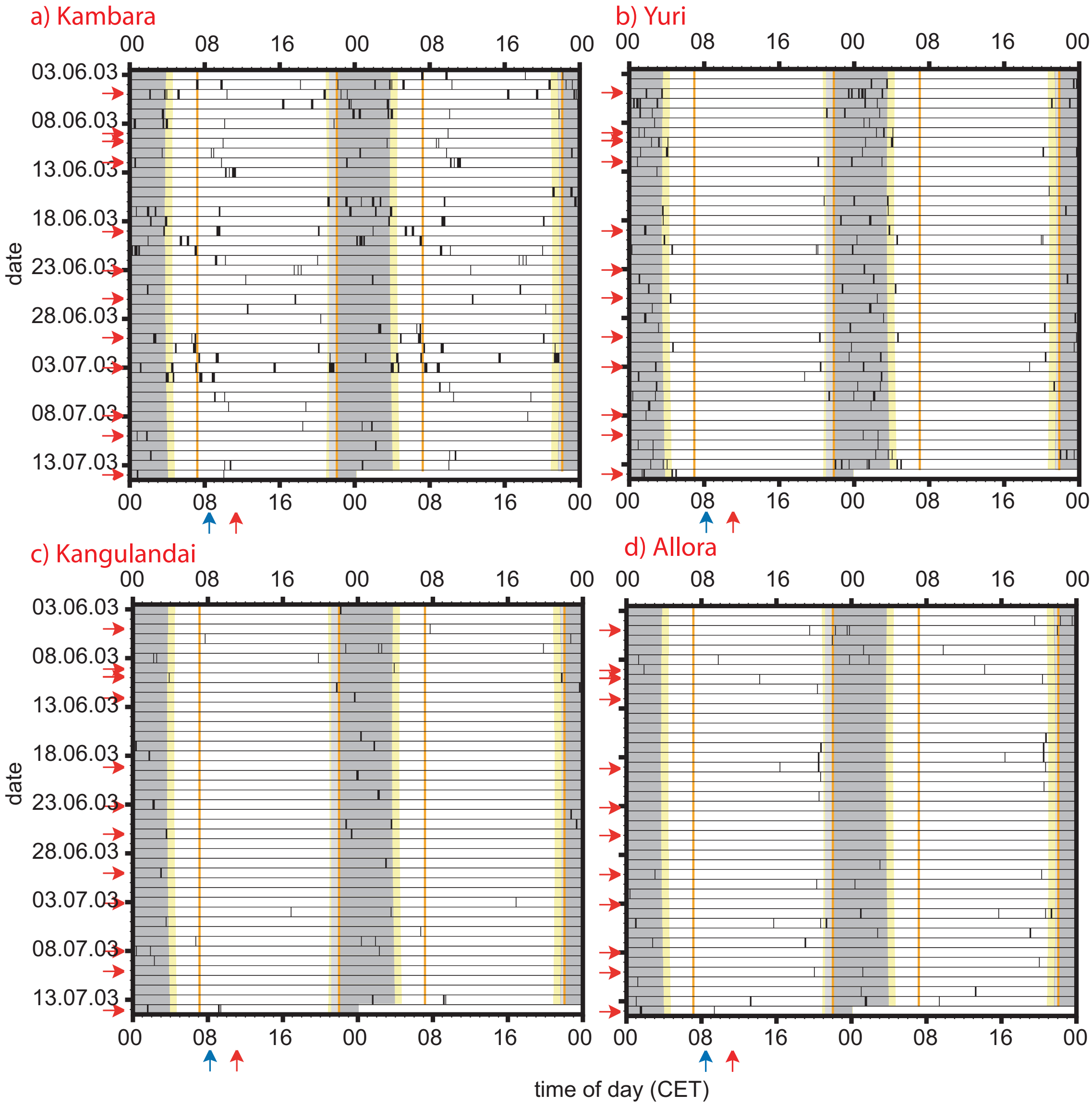

Figure 3.29: Presence on ground for all Duisburg koalas in Northern summer.
Double-plotted chronoethograms from 03 June to 14 July 2003. Black bars indicate presence on ground. For further details see Fig. 3.23.
Kambara (a) showed no distinct day-night pattern, but there were three periods when he came to the ground more regularly. The females (b-d) were on the ground mainly during the night, a pattern that was most pronounced in *Yuri*.

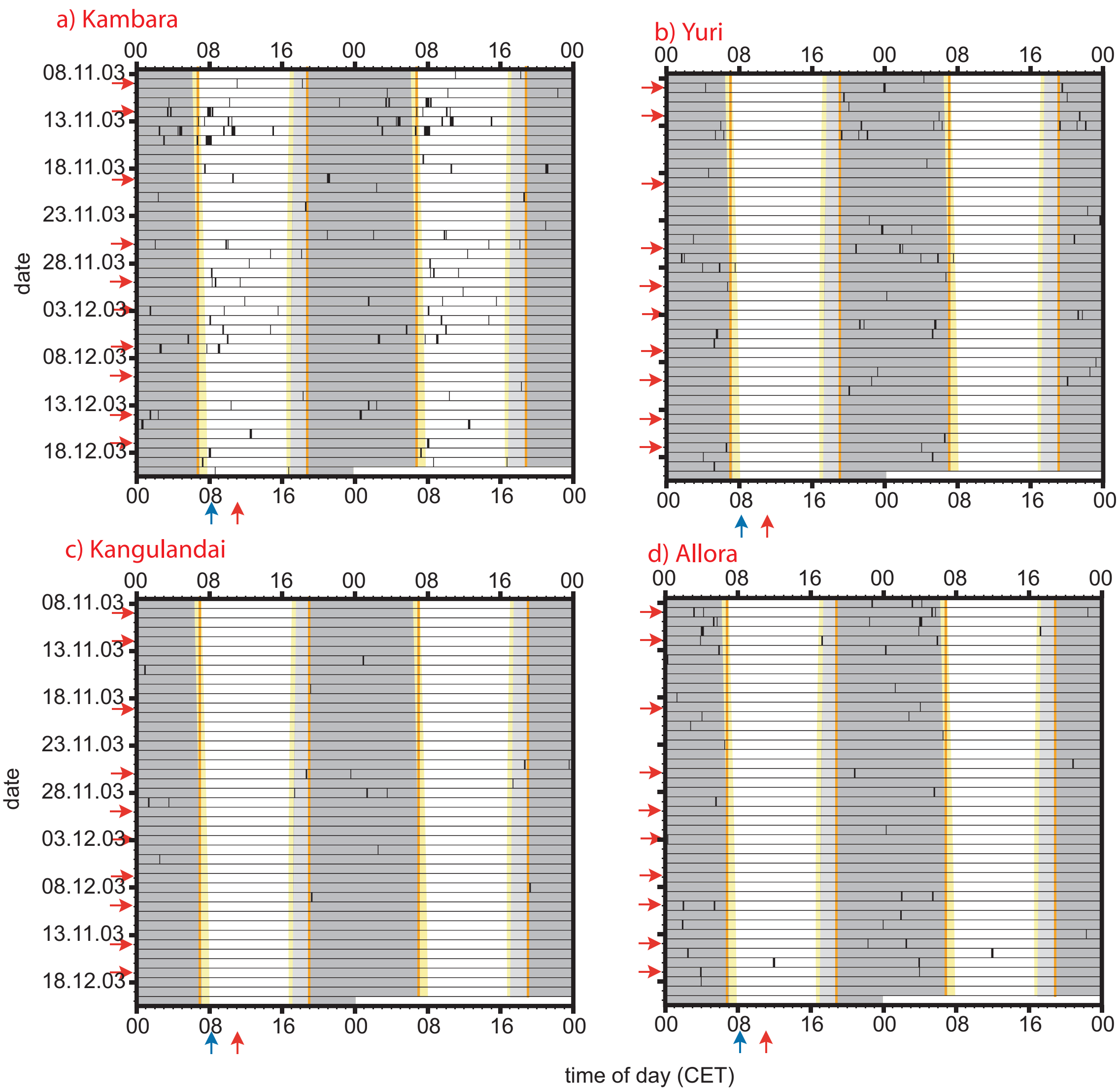

Figure 3.30: Presence on ground for all Duisburg koalas in Northern winter.
Double-plotted chronoethograms from 8 November to 20 December 2003. Black bars indicate presence on ground. For further details see Fig. 3.23.
Kambara (a) showed no day-night pattern, but peaks at 08:00 and 10:00. The females (b-d) came almost exclusively to the ground at night.

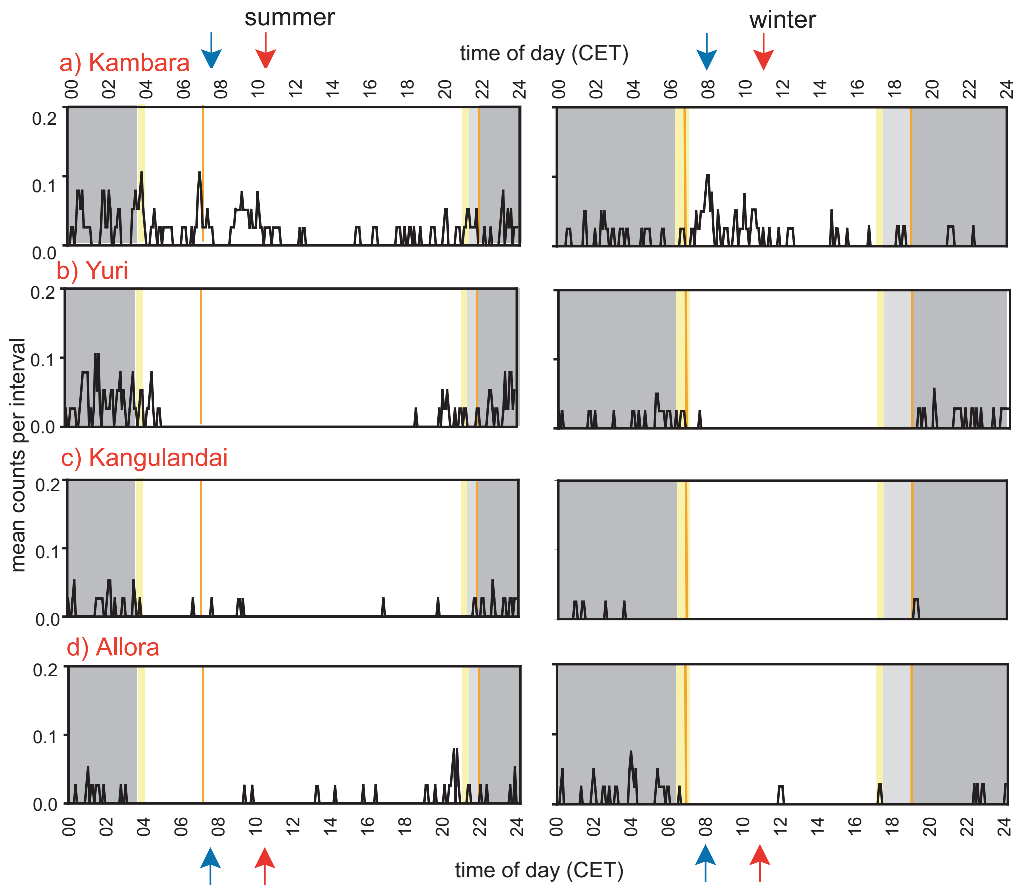

Figure 3.31: Average levels of presence on ground for all Duisburg koalas in Northern winter and Northern summer.

For details see Fig. 3.25

Kambara (a) had been observed on the ground during the complete day with some peaks in the morning. The females usually came to the ground during night and, in summer, during the early morning. Sometimes *Kangulandai* (c) and *Allora* (d) also had been seen on the ground during daytime.

3.3 Tiergarten Schönbrunn, Vienna

3.3.1 Chronoethogram and activity profiles

Total activity. *Bilyarra* showed a distinct day-night pattern of activity (Fig. 3.32). There was little activity during the day. Two slim activity bands were seen in the morning, the first while the keeper worked in the enclosure and the second, very weak one after the weighing. There were some activity bouts in the afternoon. In summer activity began in the late afternoon. In winter there was a clear onset of activity when the lights were switched off. Numerous feeding bouts followed during the night. Resting bouts between them were shorter in summer. In winter, activity ended shortly before the lights were switched on. In summer activity was prolonged into the morning until the keeper entered the enclosure.

The activity pattern of *Mirra Li*, the female was very different from the male (Fig. 3.33). There was no distinct day-night pattern, but several bands during the complete 24 hours. The highest peak in the activity profile followed the weighing and the major food presentation. Activity was also very common during the morning cleaning session. There always were feeding bouts in the afternoon at varying times. In winter the switch-off of the lights was followed by a band of activity. This was not the case in summer, when activity ended with sunrise. At this time, the only explicit resting period was observed in *Mirra Li*. It ended when the keeper entered.

Resting. Again most of the time was spent resting and the ethograms were mirror image to total activity. Therefore, resting is not discussed in detail here.

Legend for figures 3.32 and 3.33.: Double-plotted chronoethograms and activity profiles from 10 June to July 2004 (top) and 1 December 2004 to 11 January 2005 (bottom). Upper panel: chronoethogram, height of black columns indicates level of activity. Lower panel: (left) amplitude code of the plotted behaviours, (right) single-plotted activity profile (5 minute intervals) averaged over the complete observation period, same time scale as ethogram above. Background colours: dark grey = night, light grey = artificially extended day, yellow = twilight, vertical orange line= lights on / off. Blue arrow = morning cleaning and feeding (no exact time), red arrow = weighing and feeding.

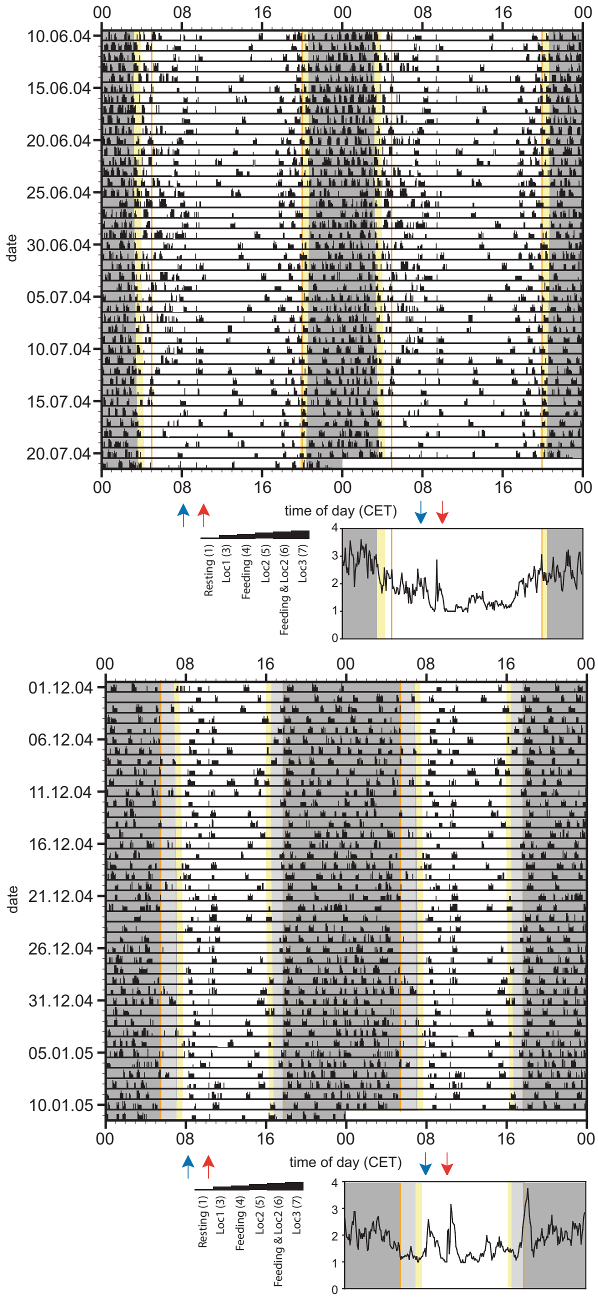

Figure 3.32: Total activity for the male *Bilyarra* at Vienna Zoo in Northern summer and Northern winter. There was a distinct day-night pattern with more activity during the night. In winter, the clearest band appeared after the lights were switched off and activity ended before natural dawn. In summer, activity began in the afternoon and was prolonged into the morning. During the day two distinct bands were visible, one during the morning cleaning session, the second one at the weighing. This was very weak in summer and consisted only of locomotor activity. In the afternoon, several feeding bouts were observed, particularly in summer.

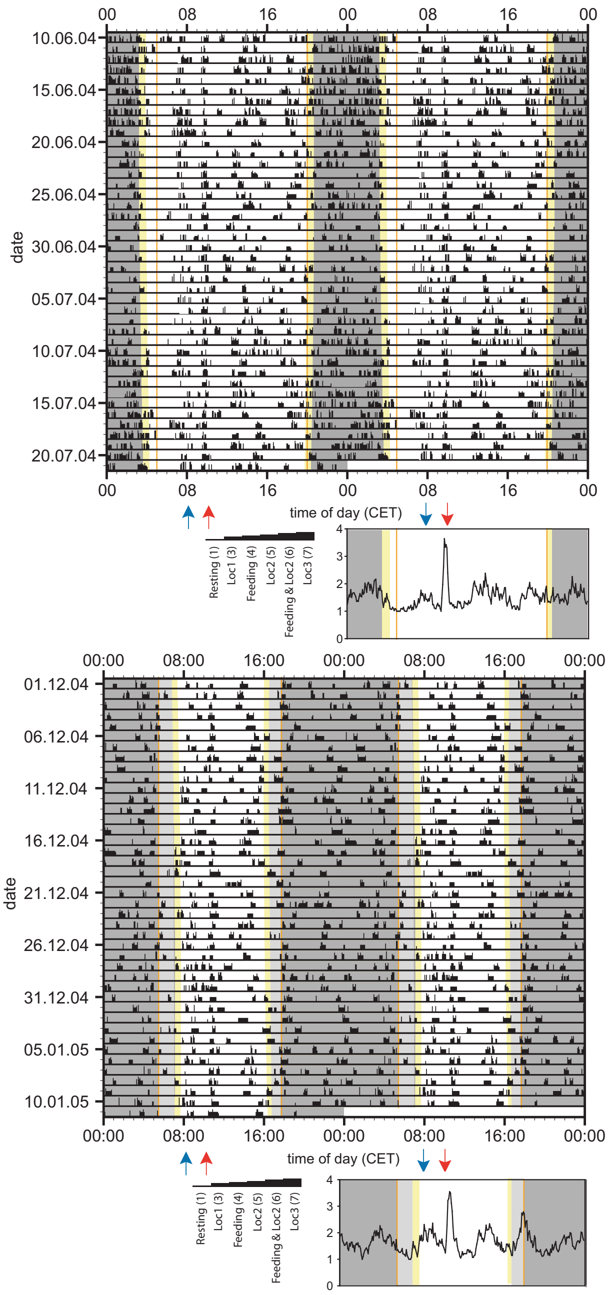

Figure 3.33: Total activity for the female *Mirra Li* at Vienna Zoo in Northern summer and Northern winter. For details see Fig. 3.32.

There was no distinct day-night pattern in *Mirra Li*. Instead, activity bouts were distributed over the complete 24 hours. In summer, there was a resting period in the morning. The clearest band of activity followed the weighing, and there was activity in the morning while the keeper was in the enclosure. Additional bouts were observed in the afternoon, at midnight and before dawn.

Feeding. During the winter-day, *Bilyarra* showed two distinct bands in feeding, one between 09:00 and 10:00 at the morning cleaning session and one after the weighing at 10:15 (Fig. 3.34a). At both times, fresh browse was introduced. Between these peaks no feeding was observed (Fig. 3.35a). One or two feeding bouts were seen every afternoon. After the lights were switched off at 18:00 a feeding bouts was seen almost daily. Frequent short bouts followed during the night until about 05:00, when feeding became very rare.

In summer, the day-night pattern was much clearer (Fig. 3.34c). Feeding was mainly reduced to the night hours, beginning about two hours before sunset and ending shortly before natural dawn. Little feeding was observed during morning until the morning cleaning session, when a slim band appeared. The activity profile showed a peak at 10:15 (Fig. 3.35c), but this was not visible as a band in the chronoethogram. Some feeding bouts were scattered through the remaining day, but generally feeding levels during the day were low.

In winter, *Mirra Li* showed a very clear band at 10:15 (Fig. 3.34b). Several feeding bouts were observed throughout the complete day, but although there were peaks in the activity profile during the morning cleaning session and in the afternoon (Fig. 3.35b), no straight band was visible. Period length τ of these feeding bouts was 3.42 hours (periodogramme, $p < 0.05$) and were probably freerunning. There was another peak after the lights were switched off. During the night feeding bouts were similarly scattered as during the day.

In summer there was almost no feeding between natural sunrise and the weighing with exception of some irregular, short bouts during the morning cleaning (Fig. 3.34d). Short bouts were observed during the remaining time, but there was no difference between the rest of the day and the night.

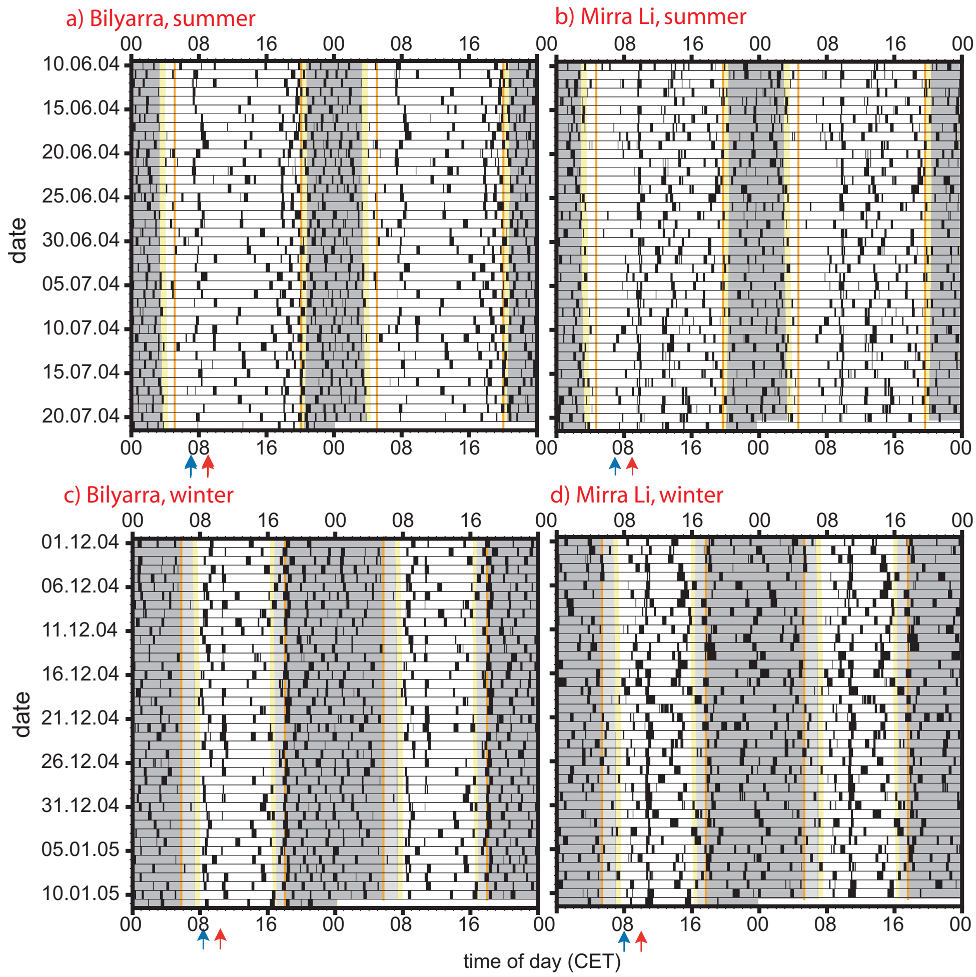

Figure 3.34: Feeding for the Vienna koalas in Northern winter and Northern summer.
Double-plotted chronoethograms from 10 June to 21 July 2004 (top) and 1. December to 11 January 2005 (bottom). Background colours: dark grey = night, light grey = artificially extended day, yellow = twilight, vertical orange line= lights on / off.
Bilyarra showed a distinct day-night pattern with a clear band after the lights were switched off, and frequent bouts during the night. During daytime there was a band at 09:00 in winter and at 08:00 in summer during the cleaning session. A second band at 10:15 was only visible in winter. In *Mirra Li* there was a clear band after the weighing and frequent feeding during the remaining day and the night. There was no feeding in the early morning.

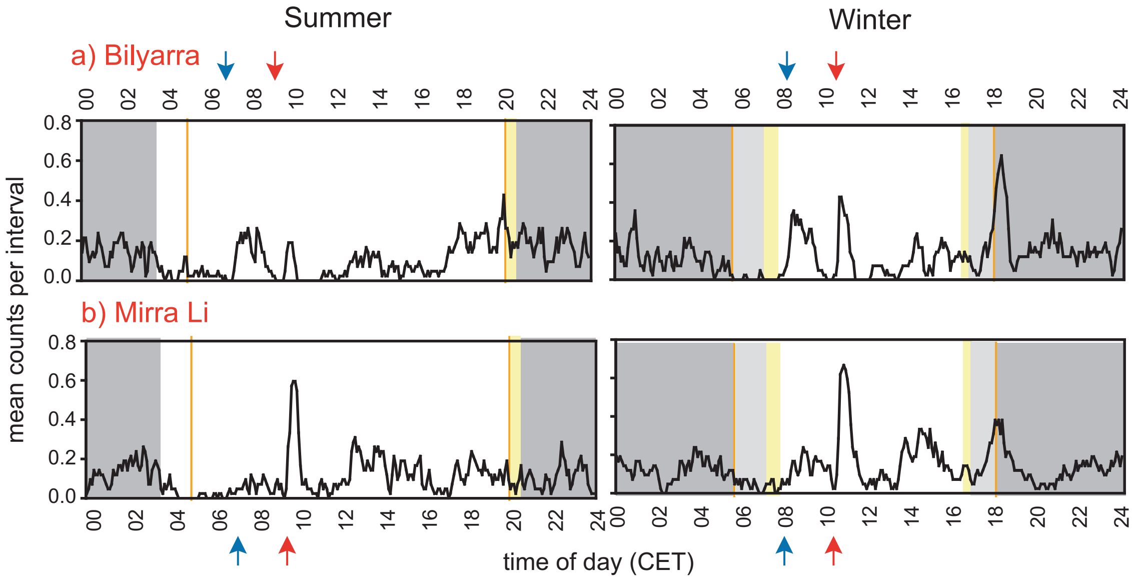

Figure 3.35: Average feeding levels for the Vienna koalas in Northern winter and Northern summer. Activity profile (5 minute intervals) averaged from 10 June to July 2004 and from 1 December 2004 to 11 January 2005. Background colours: dark grey = night, light grey = artificially extended day, yellow = twilight, vertical orange line = lights on / off. Blue arrow = morning cleaning and feeding (no exact time), red arrow = weighing and feeding.
In *Bilyarra* there were two peaks in the morning, one during the cleaning session and one after the weighing. They were stronger in winter than in summer. At night feeding levels were higher. In winter there was an additional peak after the lights were turned off. *Mirra Li* had one distinct peak after the weighing and in winter high levels in the afternoon and after the lights are turned off. There was little difference between night and day.

Locomotion. As in feeding, *Bilyarra* showed a clear distinction between day and night. In winter locomotor activity was concentrated to the nighttime (Fig. 3.36a). During the day there was one band at 10:30, after the koala had been weighed. Prior to this and afterwards, there was almost no locomotor activity. In summer locomotor activity was more common during the night (Fig. 3.36c). It was also prolonged into the morning, on several days until the keeper entered. At 09:30, after the weighing, a band is visible in the chronoethogram. The activity profile shows that locomotor activity during the day was less common than during the night (Fig. 3.37a). The differences were especially strong in summer.

Mirra Li did not show a distinct pattern in winter (Fig. 3.36b). Locomotor activity was scattered over the complete 24 hours. The activity profile shows some low, broad peaks during the morning cleaning, after the weighing and after the lights had been switched off, but levels between the peaks did not differ between day and night. In summer, there

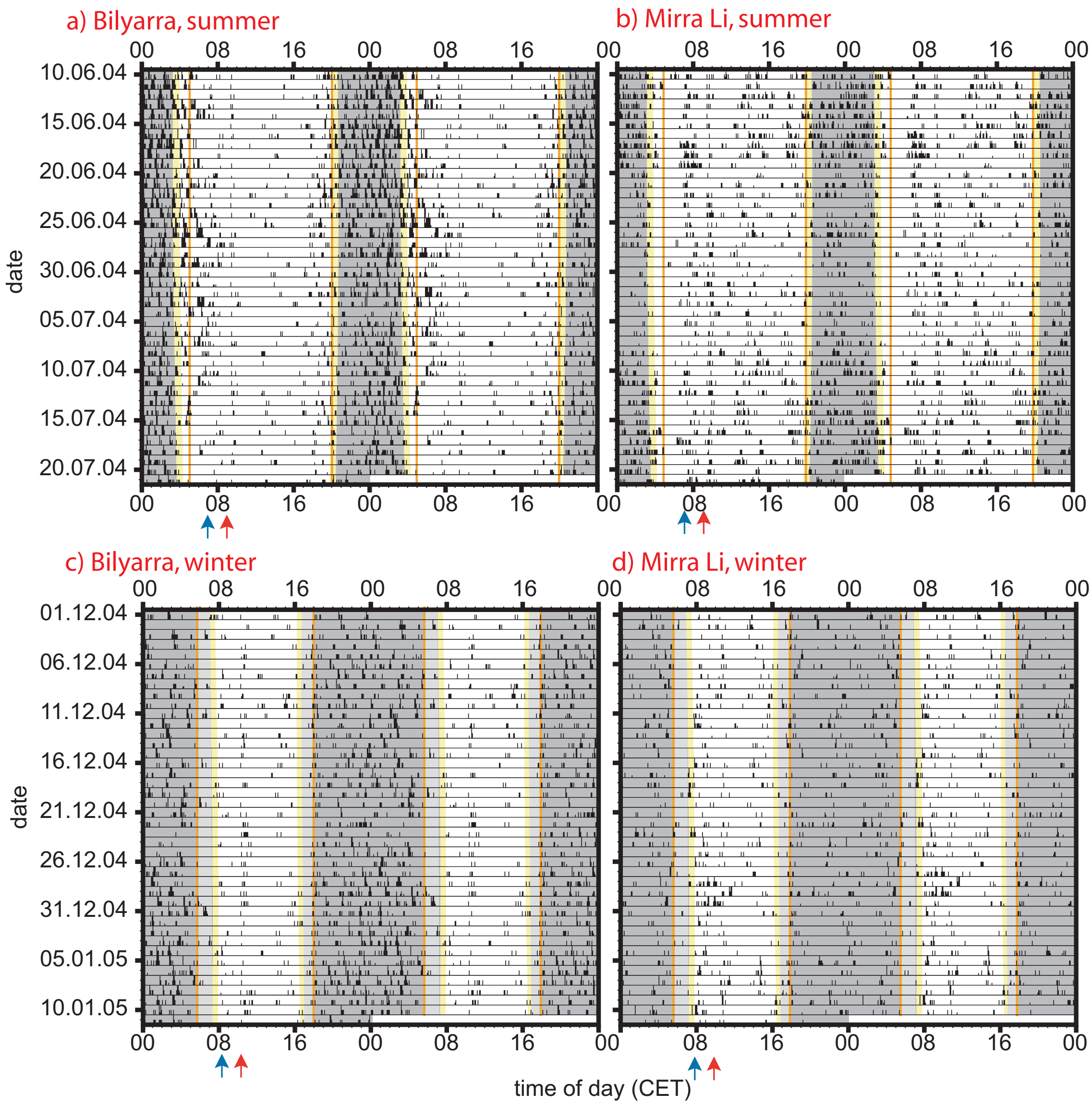

Figure 3.36: Locomotor activity for the Vienna koalas in Northern winter and Northern summer.
Upper panel: Height of the black columns indicates the level of locomotor activity (Loc1, Loc2, Loc3). For further details see Fig. 3.34.
In *Bilyarra* locomotor activity was concentrated to the night during winter. In summer it was prolonged into the morning. In both seasons there was a clear band at the weighing. In *Mirra Li* locomotor activity was distributed over the complete 24 hours with exception of the early morning in summer. In summer there were also two distinct bands, one during the morning cleaning and one after the weighing.

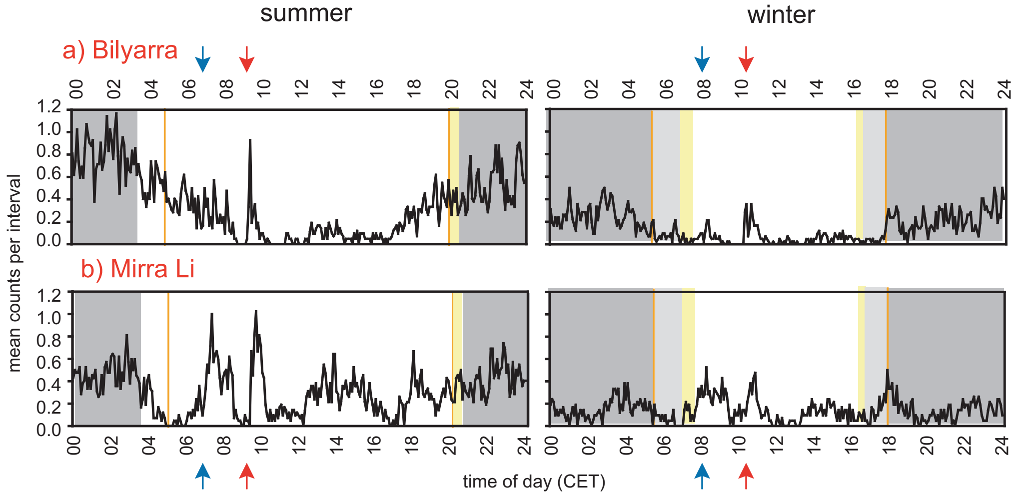

Figure 3.37: Average levels of locomotor activity for the Vienna koalas in Northern winter and Northern summer.

For details see Fig. 3.35.

In *Bilyarra* locomotor activity was generally more common during the night. There was a clear peak at the weighing time in summer. In winter this peak was lower. In *Mirra Li* locomotor activity was more common during the night in summer, but there was no clear difference in winter. In summer there were two high peaks, one at the morning cleaning and one after the weighing. Both peaks were lower in winter.

was almost no locomotor activity between sunrise and the beginning of the morning cleaning (Fig. 3.36d). Then a broad band appeared which is clearer than in winter. A second, slim band appeared after the weighing. Between these bands almost no locomotor activity had been observed. During the remaining day locomotor activity was quite frequent. The activity profile shows a small lull at 17:00, but generally locomotion levels did not change until sunrise and were not higher at night (Fig. 3.37b).

On ground. In winter, *Bilyarra* was almost exclusively on the ground during the night (Fig. 3.38a). In summer, this was extended into the morning, but usually not longer than the beginning of the morning cleaning (Fig. 3.38c). *Mirra Li* came down to the ground for short periods during the complete day. In winter, there was no difference between day and night and there were no distinct bands or peaks (Fig. 3.38b, Fig. 3.39b). In summer, she was more often on the ground during the night and the evening (Fig. 3.38d). On three consecutive days in June the chronoethogram shows a block during the morning cleaning, when *Mirra Li* was on the ground several times in succession. Even so, there was no band during the morning cleaning, although there was a band in locomotor activity (Fig. 3.39d).

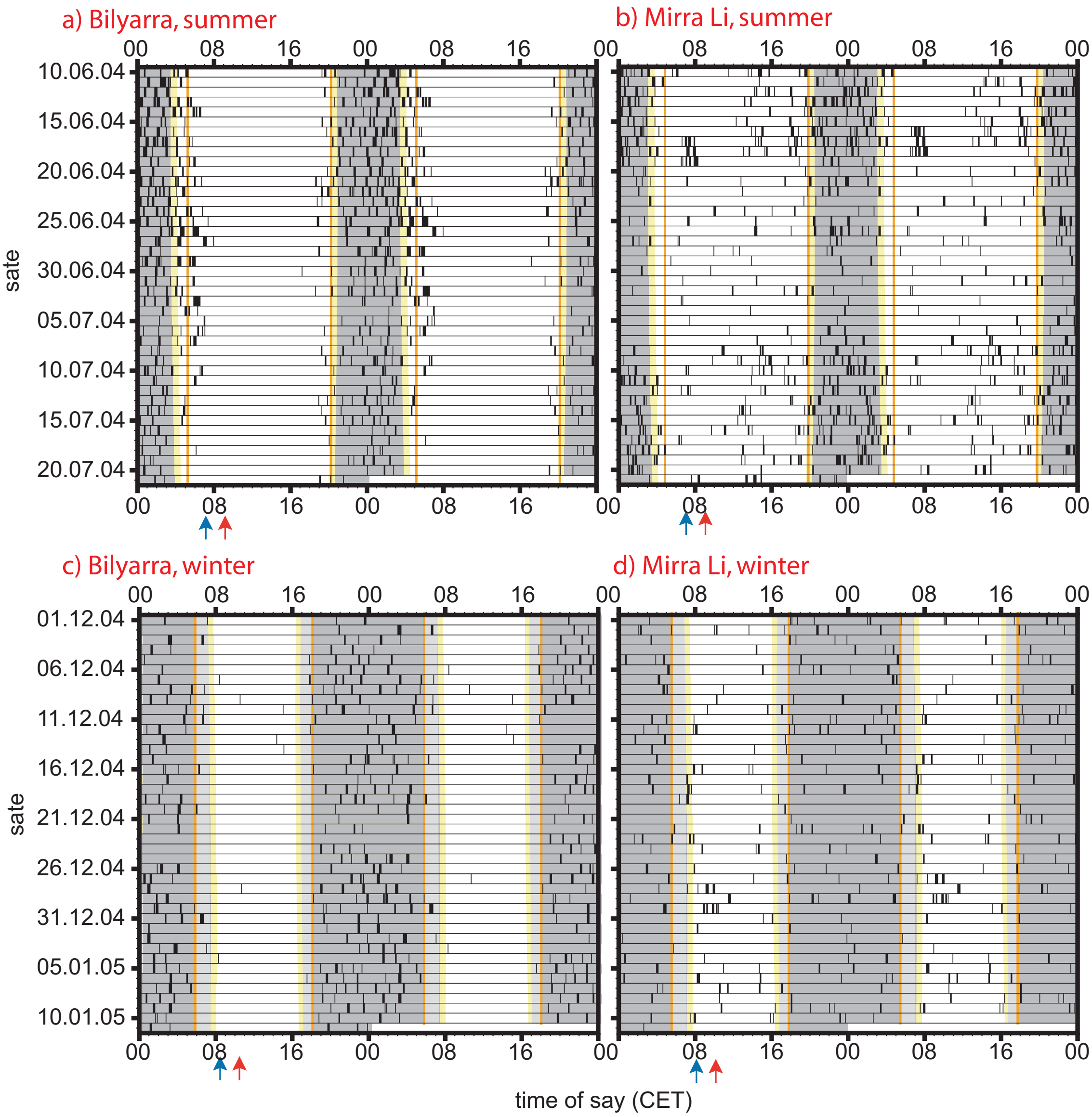

Figure 3.38: Presence on ground for the Vienna koalas in Northern winter and Northern summer.
Upper panel: Black bars indicate presence on ground. For further details see Fig. 3.34.
In winter *Bilyarra* was almost exclusively on the ground during the night. In summer this was extended into the morning. *Mirra Li* did not show a distinct pattern but was on the ground slightly more often during the morning session.

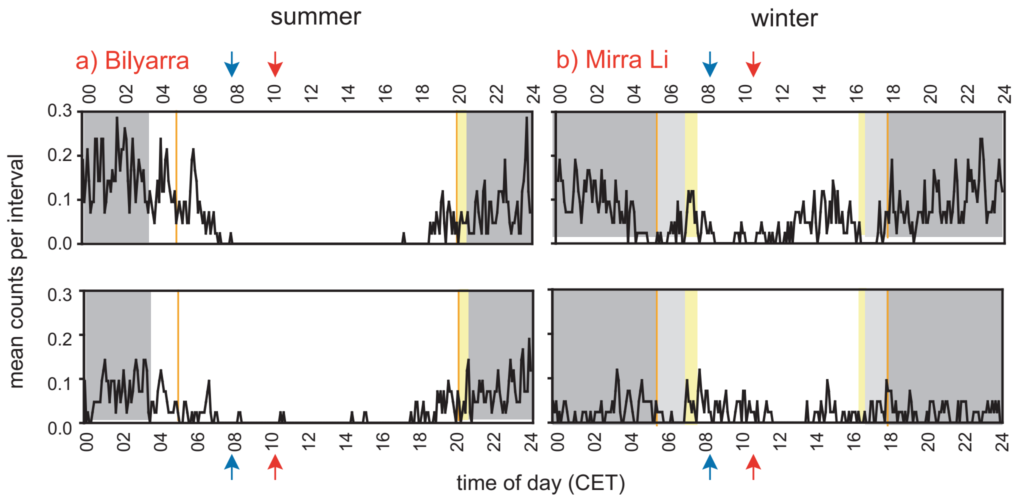

Figure 3.39: Average levels of presence on ground for the Vienna koalas in Northern winter and Northern summer.

For details see Fig. 3.35.

In winter *Bilyarra* was almost exclusively on the ground during the night. In summer this was extended into the morning. *Mirra Li* did not show a distinct pattern but was on the ground slightly more often during the morning session.

3.4 Comparison Koala Walkabout (Sydney) – Duisburg Zoo – Tiergarten Schönbrunn Vienna

3.4.1 Activity pattern

For a comparison of the three zoos, activity profiles of all koalas have been plotted for six weeks in winter and in summer each (Fig. 3.40).

Taronga Zoo is the only zoo, where all koalas had uniform activity patterns with a clear discrimination between day and night. The activity profiles reflect the patterns shown in the chronoethograms, though differences between single days are lost. At Duisburg Zoo and Vienna Zoo, patterns varied between individual koalas (Fig. 3.40b,c). Furthermore, not all koalas showed a discrimination between day and night. *Yuri* (Duisburg), *Allora* (Duisburg) and *Bilyarra* (Vienna) showed more activity during the night, while in *Kambara* (Duisburg), *Kangulandai* (Duisburg) and *Mirra Li* (Vienna) activity was displayed in short bouts throughout the complete 24 hours.

All koalas in Sydney rested during the morning, even while the keeper was inside the enclosure (Fig. 3.40a). In Duisburg and Vienna fresh browse was introduced in the morning. In Duisburg this resulted in activity in *Kambara* and *Kangulandai*, but rarely in *Yuri* and *Allora* (Fig. 3.40b). In Vienna both koalas were active while the keeper was

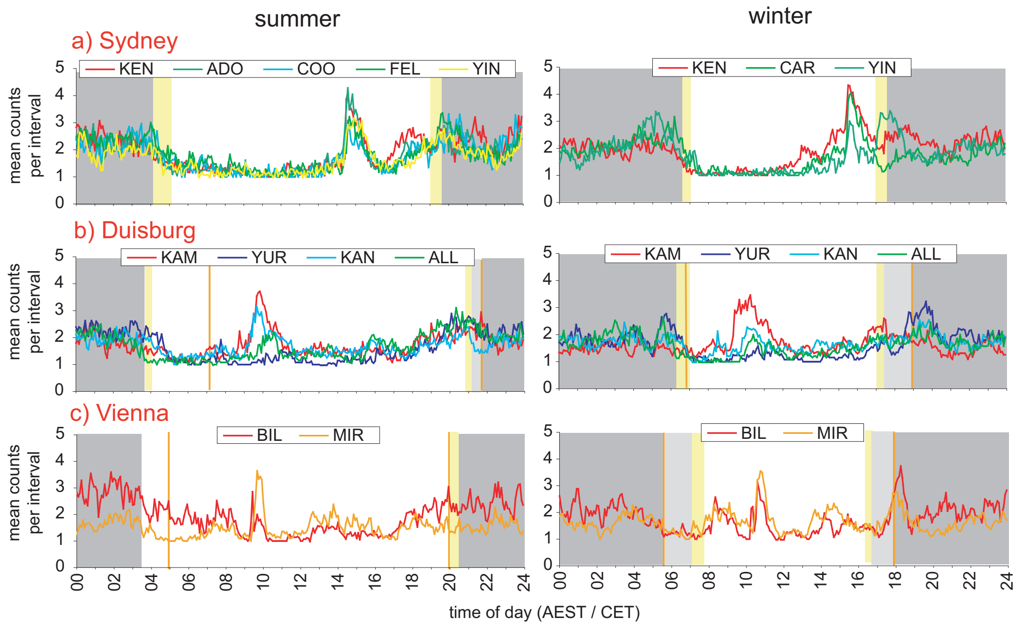

Figure 3.40: Average levels of activity for all observed koalas in summer and winter.
Activity profile (5 minute intervals) averaged over 42 days each. Background colours: dark grey = night, light grey = artificially extended day, yellow = twilight, vertical orange line = lights on / off.
In all profiles there are clear peaks at feeding times and in (b) and (c) during the morning cleaning. In winter there was an increase of activity after sunset in (a) and after the artificial lights have been switched off in (b) and (c). In summer, activity increased in the late afternoon and remained high until sunrise, with the exception of the Vienna female *Mirra Li*.

inside the enclosures (Fig. 3.40c). These koalas were weighed daily, which again resulted in some activity, particularly in the female *Mirra Li*.

In the afternoon, activity increased in Sydney and peaked at 15:30, when the keeper introduced fresh browse (Fig. 3.40a). Feeding activity was high within the next hour.In Duisburg and Vienna, feeding activity in summer also increased during the afternoon, especially after 18:00, although there was no external stimulus (Fig. 3.40b,c). In winter, most koalas displayed an activity peak at sunset or when the lights were switched off; in summer, this was only seen in some koalas. At night, activity was higher in all koalas but *Mirra Li* and *Kambara* in winter.

3.4.2 Time Budget

In all zoos, most of the time was spent resting (Fig. 3.41a). Resting times ranged from 74.1% of the day in the Sydney male in winter to 81.7% in the Vienna female in summer. Generally the Sydney koalas were the most active ones, but the difference to the other zoos was not always significant. The males were slightly, but not significantly more active during summer. This was also the case for the females in Sydney and the one female in Vienna, but not for the females in Duisburg.

Feeding was the most common active behaviour, accounting for 10.7% in the Vienna female to 17.3% in the Duisburg male (Fig. 3.41b). Differences between zoos were pronounced. The females at Duisburg Zoo fed significantly longer than the other females. In winter, feeding times were significantly longer than in summer. The males at the two European zoos did not have any seasonal differences. The Duisburg male fed significantly longer than the Vienna one and, in summer the Sydney one. In winter, the Sydney male fed significantly longer than in summer (Fig. 3.8a) and also as the other males.

The relations of the three levels of locomotor activity were similar between zoos (Fig. 3.42). All levels of locomotor activity were lowest at Duisburg Zoo. The male as well as the females showed significantly less locomotor activity than the koalas at the other zoos. The proportions between Taronga and Vienna Zoo depended on level and season. Loc1 was a rare behaviour (Fig. 3.42a). The females in Sydney displayed Loc1 significantly longer than the Vienna female, the Sydney male significantly shorter than the Vienna male, but differences were only small.

Loc2 was in all koalas the most common level of locomotor activity (Fig. 3.42b). Again it was observed for the shortest duration in Duisburg Zoo. The male in Sydney and Vienna did not differ from each other. Significant differences have been found in the females in Sydney and the Vienna female. In winter the Sydney females showed more locomotor activity than *Mirra Li*, but in summer *Mirra Li* showed more than twice as much Loc2 than in winter and significantly longer than the Sydney females.

Loc3 was observed for the shortest duration than Loc2, but the pattern in the zoos was the same (Fig. 3.42c). However, it is much rarer in Duisburg than in the other zoos. In winter Loc3 is slightly, but not significantly more common than in Vienna. In summer it was the other way round, when the Vienna male showed more than twice as much Loc3 than in winter.

The time spent on the ground showed a similar pattern as locomotor activity (Fig. 3.41c). The Duisburg koalas came to the ground for the shortest time in both seasons. The male at Taronga Zoo was on the ground for the longest time, but the difference to the Vienna male was smaller in summer, when the Vienna male was on the ground significantly longer. Different from the males the Sydney females were on the ground for a shorter time than the Vienna female. Like the Vienna male, the female was significantly longer on the ground in summer than in winter.

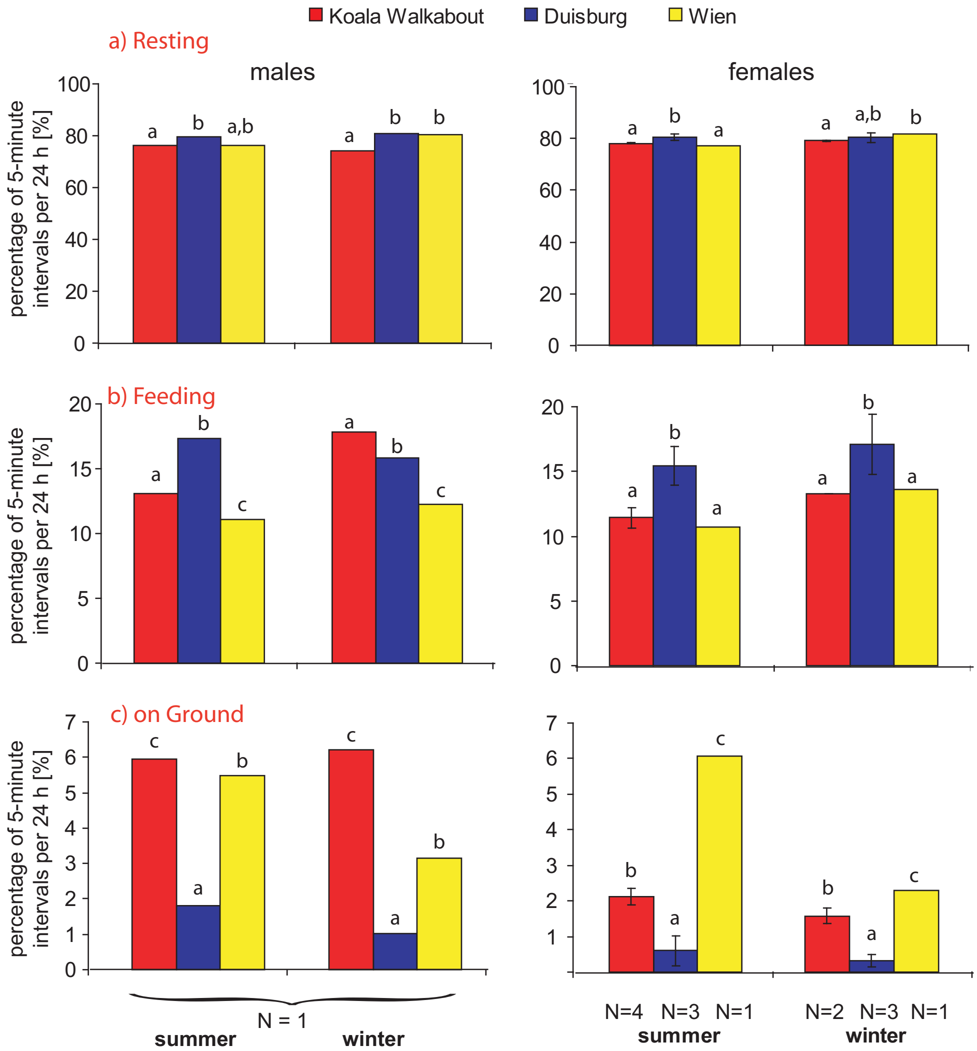

Figure 3.41: Average daily time budget for resting, feeding and presence on ground of the koalas at Koala Walkabout (Sydney), Duisburg Zoo and Vienna Zoo.

Percentage of 5 min observation intervals per 24 hours, values are based on 42 days each in summer and winter. Means are calculated for individual koalas with exception of the females in Sydney and Duisburg (number of females is given in diagram). In this case standard deviation is given between individual means. Letters indicate significant groups, $p < 0.05$.

The koalas at Sydney were generally more active than the European ones. The highest amount of feeding time has been observed at Duisburg Zoo, the shortest at Vienna Zoo. The Sydney koalas were to the ground for the longest, the ones at Duisburg for the shortest time.

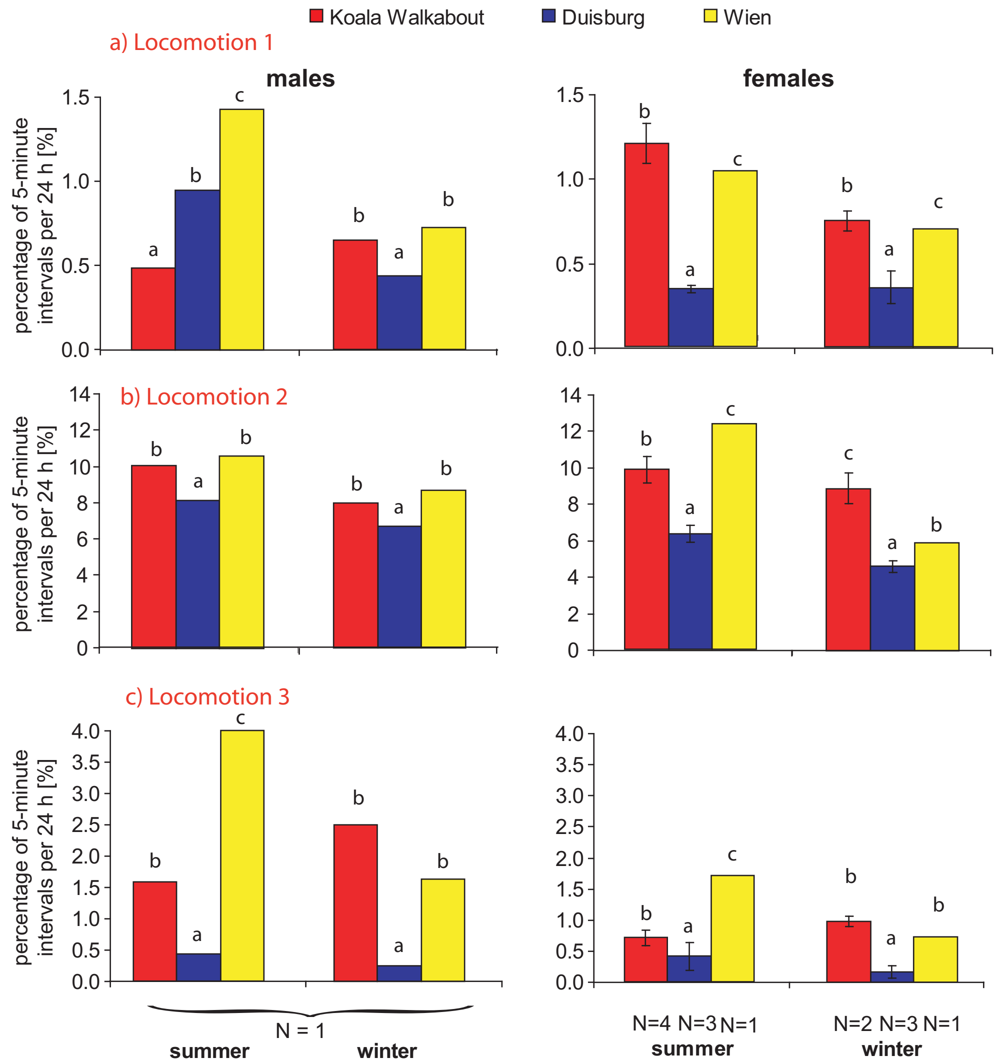

Figure 3.42: Average daily time budget for locomotor activity of the koalas at Koala Walkabout (Sydney), Duisburg Zoo and Vienna Zoo.

For details see Fig. 3.41. The koalas at Duisburg Zoo showed the least amount of locomotor activity, especially in Loc3. Loc3 was most common in Vienna. Loc2 was similarly often observed in Vienna and Sydney, while Loc1 was generally more common in Vienna, but in the males there were strong differences between the seasons.

3.4.3 Day:night ratio

The day:night ratio describes how much of the behaviour has been displayed during night or day in relation to day length. Resting was almost equally distributed between night and day in all koalas (Fig. 3.43a). However, most koalas rested slightly more during the day with exception of the Duisburg male and the Vienna female. In summer, there was significantly more resting during the day than in winter in the Vienna koalas and some of the Duisburg koalas.

Feeding was usually more often observed during the night, particularly in the females in Sydney and Duisburg (Fig. 3.43b). In summer, when nights were considerably shorter, there was relatively more feeding during daytime than in winter. This was strongest in *Ken*, who actually had a positive day:night ratio in summer. In *Kambara* and *Mirra Li*, more feeding took place during daytime in winter.

Locomotor activity was more common during the night, but not in *Kambara* (Fig. 3.44). Like feeding, it was more often observed during daytime in winter than during night. In *Mirra Li*, the differences between day and night were not as strong as in the other koalas too. Loc3, the highest level of locomotor activity, was in all koalas relatively more often observed during the night than during the day. In some koalas it was almost never seen during the day.

The presence on the ground showed a similar pattern as locomotor activity (Fig. 3.43c). All koalas but *Kambara* came to the ground more often during the night. This was especially strong in the females in Sydney and Duisburg. Only *Kambara* was generally seen on the ground more often during daytime.

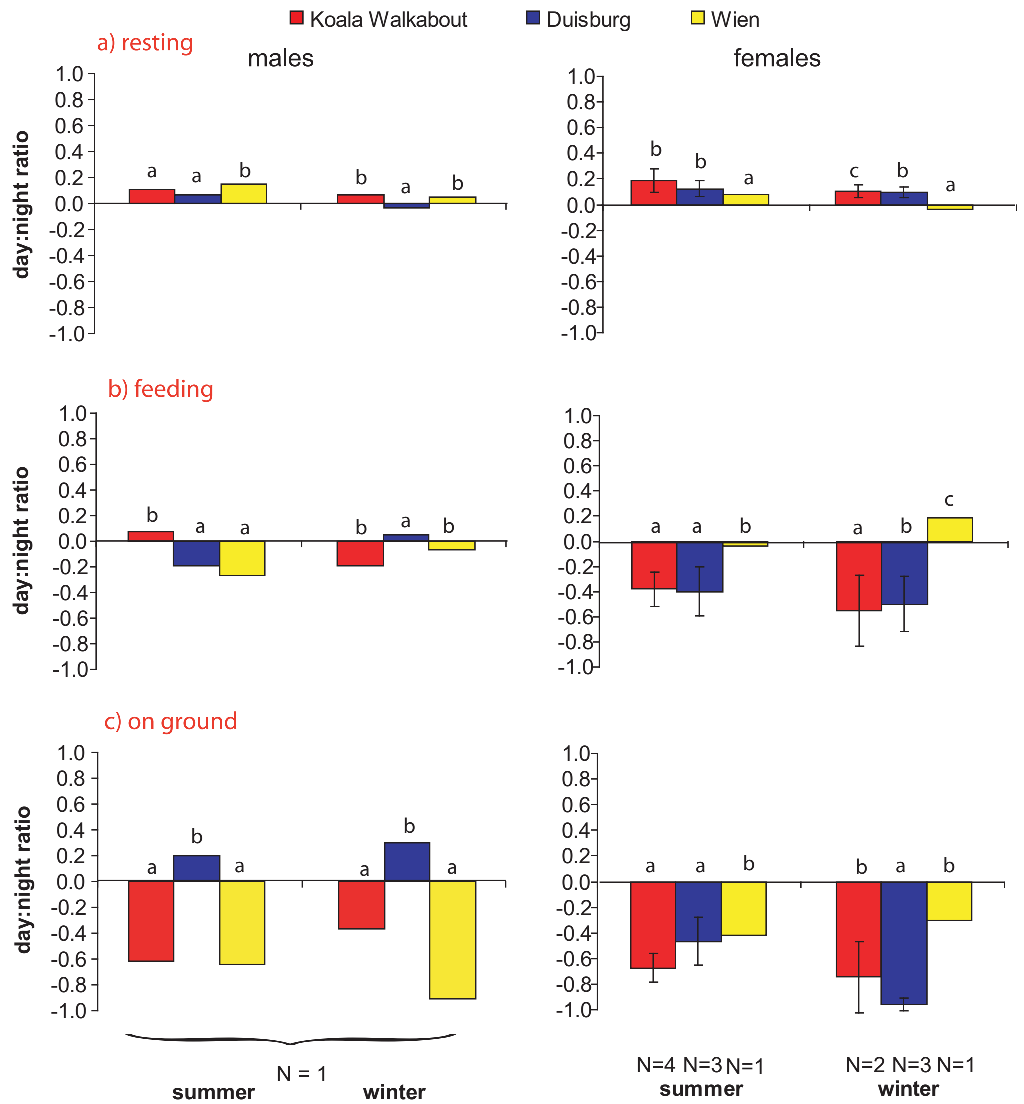

Figure 3.43: Average day:night ratio for resting, feeding and presence on ground of the koalas at Koala Walkabout (Sydney), Duisburg Zoo and Vienna Zoo.

Positive values indicate that behaviour was more often observed during the day, negative value that is was more often observed during the night. Letters indicate significant groups, $p < 0.05$.

Resting was only slightly more common during daytime in most koalas. In summer there was slightly more resting during daytime than in winter. Feeding was more common during the night in most koalas, especially the Sydney and Duisburg females. There were distinct individual differences between seasons. Mostly the koalas came to the ground during the night, with exception of the Duisburg male.

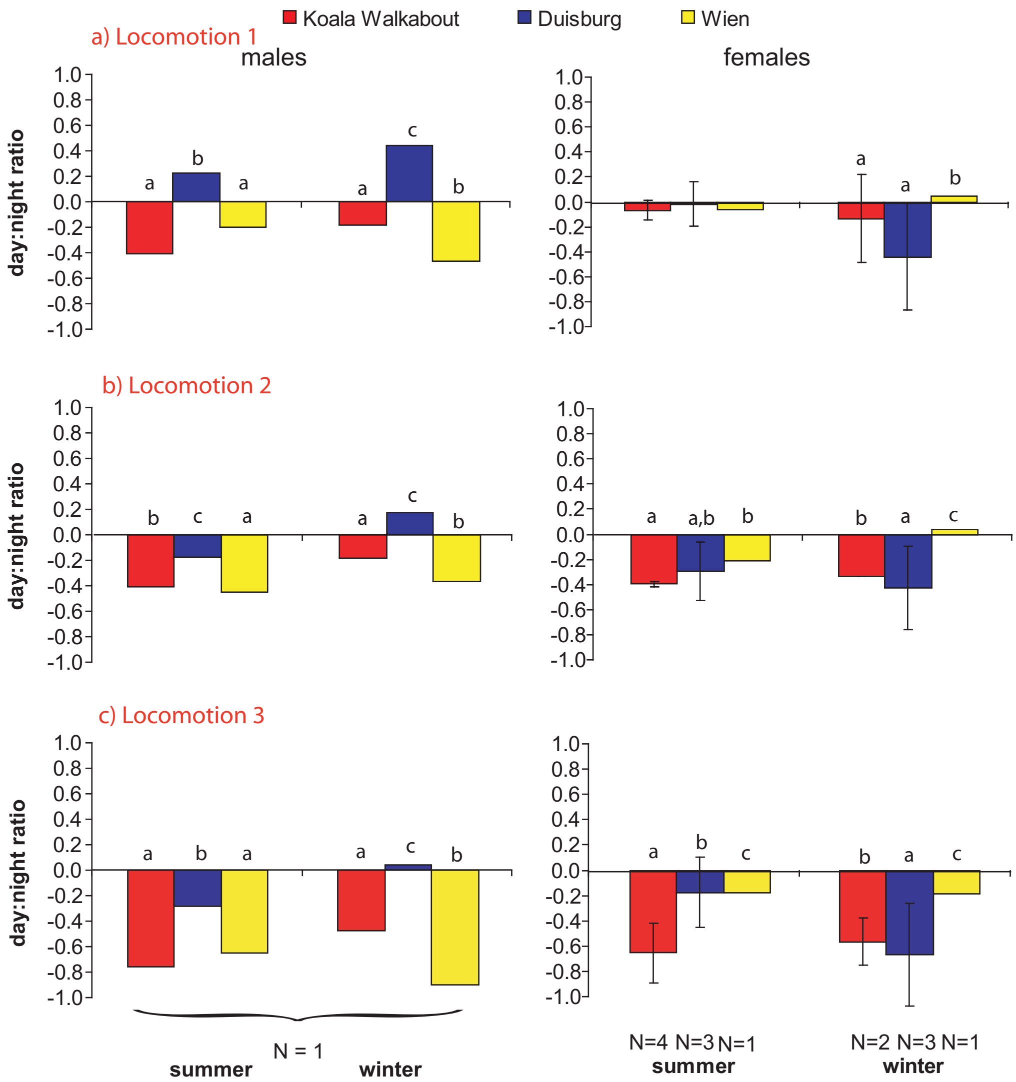

Figure 3.44: Average day:night ratio for locomotor activity of the koalas at Koala Walkabout (Sydney), Duisburg Zoo and Vienna Zoo.

For details see Fig. 3.41. With exception of *Kambara* and *Mirra Li*, locomotor activity was more common during the night.

3.4.4 Feeding bouts

Feeding bouts are a good parameter to measure periods of activity in koalas and have been used in free-range studies before (Robbins & Russell 1978; Logan & Sanson 2002a, 2003). The koalas at Duisburg Zoo spent the highest amount of time per day feeding (Fig. 3.45). The actual number of bouts per day does not differ from Sydney, where koalas spent less time feeding, but single bouts in Duisburg had on average a longer duration than at the other zoos. Vienna had the shortest feeding times in this study and also the shortest and most feeding bouts per day. This is clearly visible in the chronoethograms for feeding (Figs 3.15, 3.23, 3.24 and 3.34).

The variation between single feeding bouts during the day differed strongly. Therefore the mean value might not be the only useful measure for the duration. A histogram of bout duration gives a more complex picture (Fig. 3.46). At Vienna Zoo short feeding bouts were very common. 75% of the bouts lasted only five intervals (25 min) or less. The longest observed bout lasted 15 intervals (75 min). At Sydney and Duisburg Zoo short bouts were also more common than long ones, but 25% of the bouts lasted at least eight intervals (40 min) in Sydney and nine intervals (45 min) in Duisburg. At Sydney Zoo the longest observed bout lasted 24 intervals (120 min), and at Duisburg Zoo even 29 intervals (145 min), which is almost twice as long as the longest bout in Vienna.

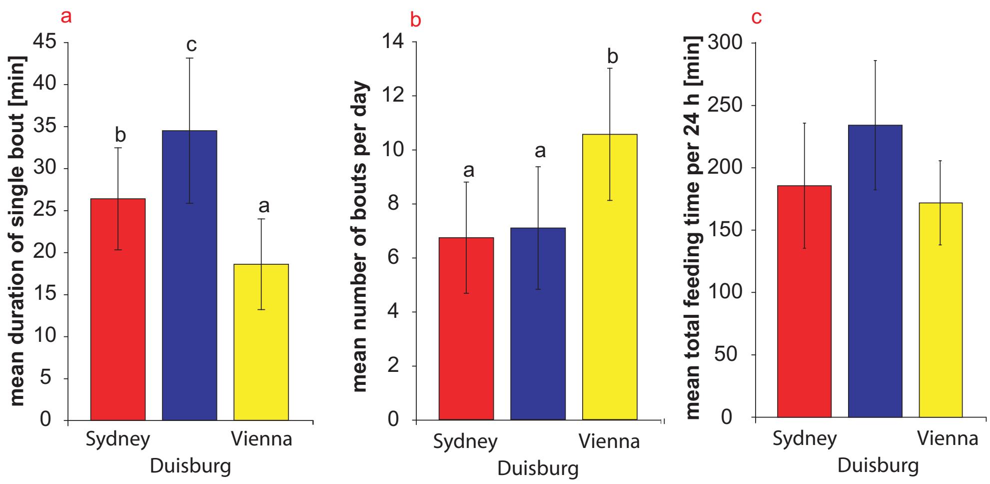

Figure 3.45: Average duration of single feeding bouts, number of feeding bouts per day and average daily feeding time.

Based on six weeks each in summer and winter, values for males and females are combined. Values for five koalas in Sydney, four koalas in Duisburg, two koalas in Vienna, number of observed feeding bouts N_{SYD} = 2157, N_{DUI} = 2377, N_{VIE} = 1770. Bars give standard deviation between single bouts (a) respectively days (b,c). Letters indicate significant groups, $p < 0.05$.

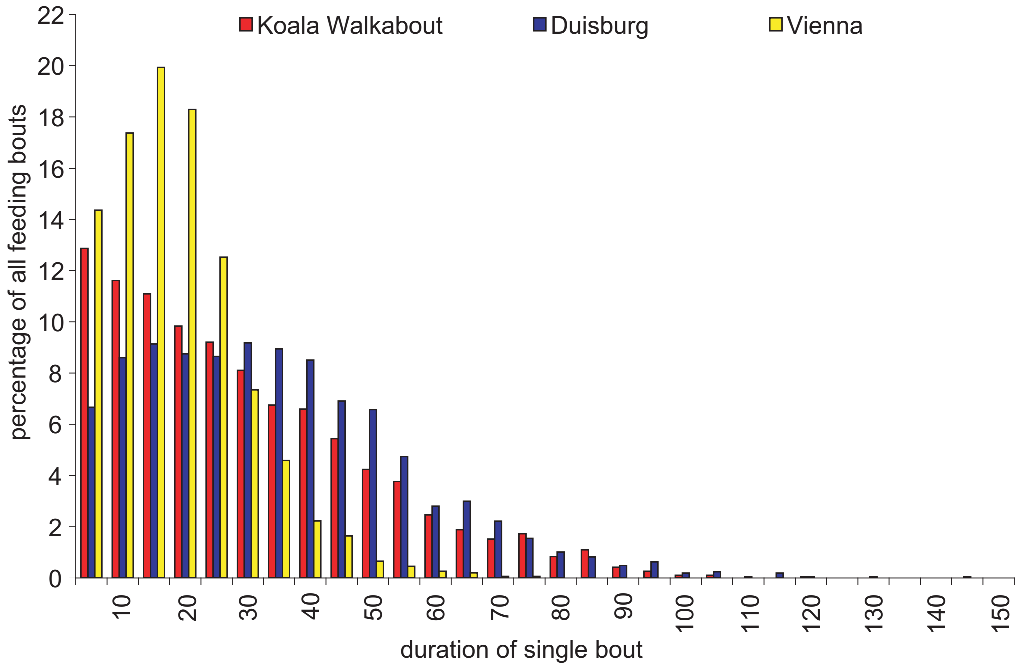

Figure 3.46: Duration of feeding bouts.
Histogram calculated from all feeding bouts observed within six weeks in summer and winter. Values of one male per zoo, four females in Sydney, three females in Duisburg and one female in Vienna, values of males and females are combined. Number of observed feeding bouts N_{SYD} = 2157, N_{DUI} = 2377, N_{VIE} = 1770.
At Duisburg Zoo long bouts are more common than at the other zoos. Vienna had the highest amount of short bouts. Furthermore, the longest bouts have been observed at Duisburg Zoo. Koalas at Vienna Zoo displayed no bouts longer than 80 minutes.

3.5 Influence of light

Light regime varied between zoos in day length and seasonal variations. In Sydney, for most of the year the koalas experienced natural sunlight with seasonal variations. In Vienna, natural light was provided through large skylights. Additionally artificial lights were used to illuminate the indoor enclosure and prolong the day during winter. In Duisburg natural light was provided through frosted sky-lights and additionally the enclosure was illuminated by lights. The lights extended the days in winter and the evening slightly in summer. Day lengths, durations of twilight and artificial light regimes are given in Table 3.1.

	Sydney	Vienna	Duisburg
shortest day	07:00 – 16:53	07:43 – 16:03	07:58 – 16:40
	9 h 53 min	8 h 20 min	8 h 42 min
longest day	04:41 – 19:06	03:54 – 19:59	03:34 – 20:41
	14 h 25 min	16 h 25 min	17 h 07 min
shortest artificial day	—	12 h 20 min	12 h 00 min
longest artificial day	—	15 h	$\sim$ 18 h (begins with sunrise)
artificial lights in winter	—	05:30 – 17:50	07:00 – 19:00
artificial lights in summer	19:00 – 20:30	05:00 – 20:00	07:00 – 22:00
duration natural dawn	24 – 30 min	31 – 42 min	21 – 52 min
duration natural dusk	24 – 30 min	31 – 42 min	31 – 61 min

Table 3.1: Day length, twilight and artificial light regimes at the studied zoos.

In Sydney, there was little activity in the morning in both seasons (Fig. 3.40a). Activity increased in the afternoon and peaked at the Keeper's Talk. In summer, activity reached a lull between 16:00 and 17:00, in winter this lull was much shorter. In summer, activity first dropped at sunset but increased again during dusk. In winter, there was a high increase in activity at sunset for about one hour in *Yindi*. A smaller increase was visible in *Ken* too. In *Carrie* activity increased only slightly after dusk. Activity ended with sunrise in summer, in winter there was an activity peak in the last hours before the beginning of dawn. During dawn, activity was reduced and the koalas rested after sunrise.

In Duisburg, patterns varied between individuals (Fig. 3.40c). All koalas rested after sunrise in summer. In winter, there was a small activity peak in *Kangulandai* and *Kambara* during natural dawn. In summer, there was a slight increase when the lights were switched on at 07:00. At both times, the keeper was usually in the enclosure. Activity increased in the afternoon. In summer a peak was reached shortly before sunset and activity decreased again when the lights were switched off. In winter, activity in all koalas increased during natural dusk, was reduced again and reached a high peak around the time when the lights were switched off again. The females displayed another peak between 05:00 and 07:00, before the lights were switched on, then activity ceased. In summer, activity ended with the beginning of dawn in *Allora* and with sunrise in the other koalas.

In Vienna, there was some resting after dawn in summer, but not in winter (Fig. 3.40b). In summer, activity increased in the afternoon towards dusk with a peak at the time after the lights were switched off. It remained on this level during the night. In winter, no change in activity was seen at sunset/dusk, but there was a high peak about one hour after the lights have been switched off. Activity slowly decreased in the last two hours of the night in winter, and increased slightly during dawn. In summer, it ended more abruptly with dawn in summer in *Mirra Li* and after the artificial lights had been switched on in *Bilyarra*.

3.6 Influences of keepers and handling

3.6.1 Sydney Koala Walkabout (Taronga Zoo)

A keeper enteres the enclosure three times a day on a regular basis, at 07:00 in the morning for cleaning the floor, between 14:00 and 15:30 to remove old browse and at 15:30 to provide fresh browse at the beginning of the Keeper's Talk. In irregular intervals (between one and four months) all koalas are caught for a weighing. In the females also the pouches are checked for joeys. To analyse the reaction of the koalas to these events, their behaviour was plotted as Pre-/Post-Stimulus-Time-Histograms (PSTH), showing the level of activity prior and after the action of the keeper.

Morning cleaning. Although the chronoethogram shows no band at 07:00, there was a small peak in locomotor activity of the females in the PSTH from 06:35 to 07:25 (Fig. 3.47). In most cases the koalas were out of reach of the keeper. Two of the females, *Lowanna* and *Yindi* were observed to occasionally approach the keeper. The keeper picked them up and carried them around for a few minutes. Both koalas had been kept at the Education Centre before, where they had been trained for handling and visitor contact. The other koalas at Koala Walkabout were not used to such handling.

Activity generally decreased between 05:00 and 07:00. This decrease stopped in the females about 30 minutes prior to the morning cleaning season, when locomotor activity slightly increased. The increase stopped five minutes after the keeper entered the enclosure and decreased while the keeper still worked there. In *Ken*, no changes were visible in the PSTH.

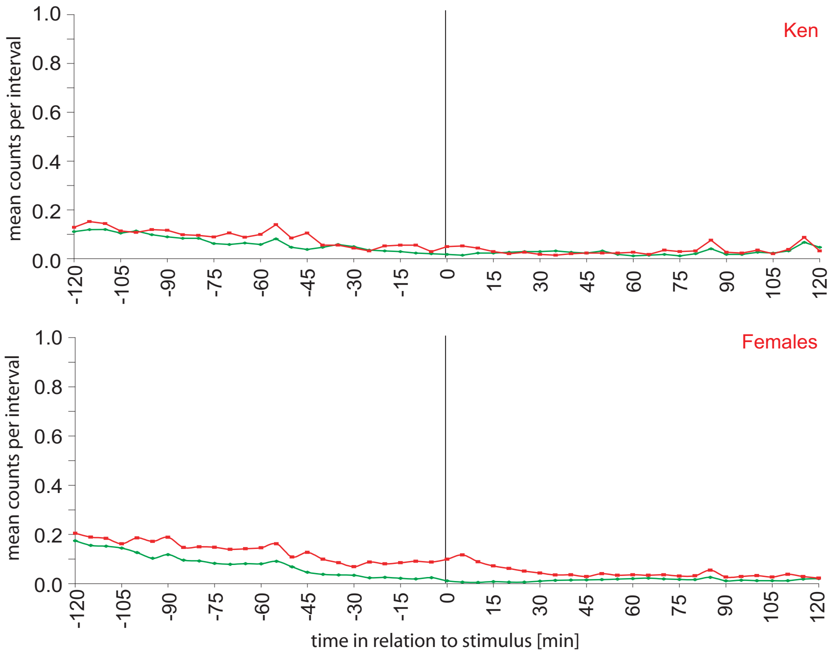

Figure 3.47: Time relation of feeding and locomotor activity to the morning cleaning session. PSTH for morning cleaning session during six weeks each in summer and winter for *Ken* and the females (N_{sum}= 4, N_{win}= 2). 0 indicates the time the keeper entered the enclosure for cleaning the floor (07:05 $\pm$ 8 min). During this time contact with the koalas was rare. Green line = feeding, red line = locomotor activity. In the females there was a very small increase in locomotor activity; in the male *Ken* no reaction was visible.

Removal of old browse. The removal of old browse took place between 12:20 and 15:30. On some days the keeper left some branches in case a koala was feeding, but usually all browse was removed. Due to the irregularity of this action the time lapse between removal of old and introduction of fresh browse varies between single days.

Since usually all browse had been removed, feeding declined to almost zero (Fig. 3.48). The rise in feeding about 30 minutes after zero was due to the Keeper's Talk (Fig. 3.49). Locomotor activity increased during the next hour. Although some koalas moved away when the browse they were sitting in was removed, no immediate peak was shown in the PSTH.

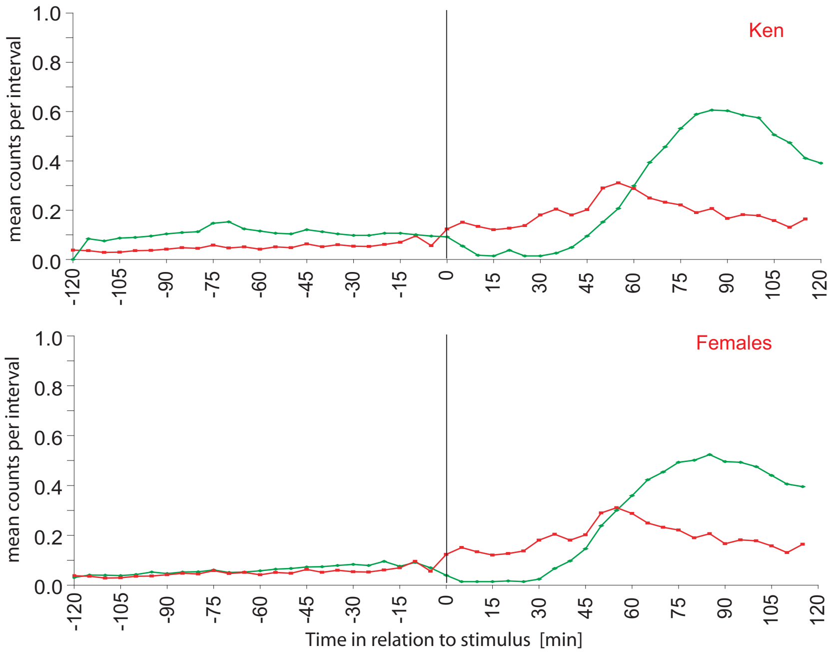

Figure 3.48: Time relation of feeding and locomotor activity to browse removal.
PSTH for browse removal during six weeks each in summer and winter for *Ken* and the females (N_{sum}= 4, N_{win}= 2). 0 indicates the time the keeper removed the old browse (14:34 $\pm$ 7.5 min); vases were empty until the beginning of the Keeper's Talk. Green line = feeding, red line = locomotor activity.
After the old branches had been removed, feeding was not possible anymore. Locomotor activity increased during the next 30 minutes, then feeding increased, which was due to fresh browse during the Keeper's Talk ((Fig. 3.49).

Keeper's Talk. At 15:30 the keeper entered the enclosure for a 15 minutes Keeper's Talk, which began with the introduction of fresh browse. Contact with the koalas was rare. The Keeper's Talk was clearly visible in the chronoethograms as an increase in activity, especially feeding. In all koalas an increase in locomotor activity was also visible in the PSTH (Fig. 3.49). However, this might be due to an overlap with the removal of the browse (see 4.6.1.2).

Immediately after the fresh browse had been put into the vases, the koalas began to feed. Feeding level stayed high for 30 to 50 minutes depending on the koala and began to fall slowly after that. *Yindi* was an exception (Fig. 3.48): although she displayed an increase in locomotor activity, feeding was almost zero in the two hours prior to the Keeper's Talk. Feeding increased slightly after fresh browse was available, but remained on a low level until dusk, when *Yindi* showed a clear band in feeding.

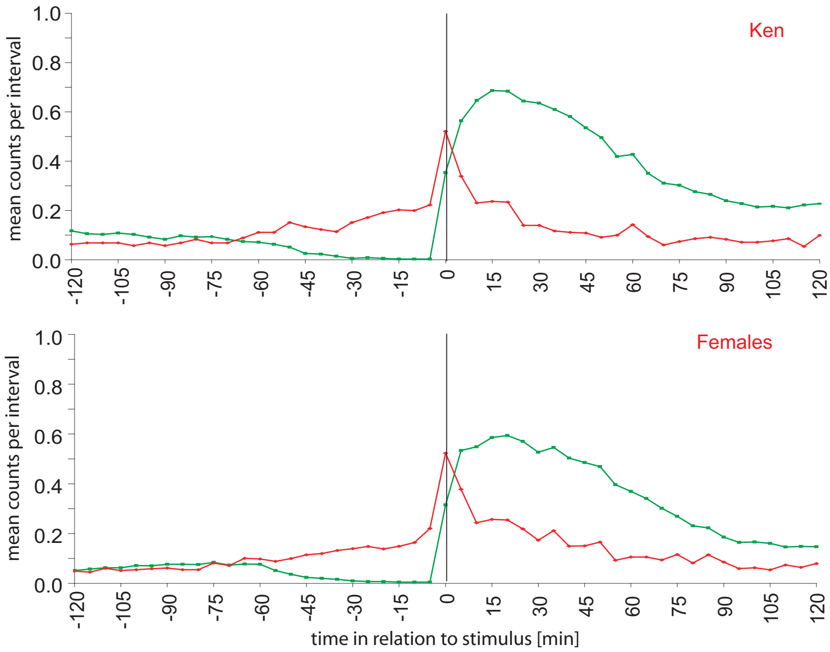

Figure 3.49: Time relation of feeding and locomotor activity to browse introduction at the Keeper's Talk. PSTH for Keeper's Talk during six weeks each in summer and winter for *Ken* and the females (N_{sum}= 4, N_{win}= 2). 0 indicates the time the keeper enters the enclosure and introduced fresh browse (15:30). During this time contact with koalas was rare. Green line = feeding, red line = locomotor activity.
Locomotor activity was increased prior to the Keeper's Talk (also see Fig. 3.48). Feeding started immediately after the fresh browse was introduced and remained high. There also was an short peak in locomotor activity.

Weighing and pouch inspection. In *Ken*, the PSTH shows an increase in locomotor activity when the keepers started to catch *Ken*, what usually took not longer than ten minutes (Fig. 3.50). *Ken* showed no aggressive behaviour towards the keeper, but often whimpered. After his release, *Ken* often stayed on the ground and appeared disorientated. Then he climbed to a fork and usually stayed there. Only on 6 March 2004 more activity has been observed within the next hour.

The females were harder to catch, therefore more locomotor activity was observed in the 10 minutes before they were caught. During pouch inspection, the females tried to free themselves by scratching and biting. The reaction afterwards differed between individuals and event, in some cases the females settled down quickly and rested for the remaining morning, in other cases higher amounts of locomotor activity were observed. These days account for the high levels within the 35 minutes after the release.

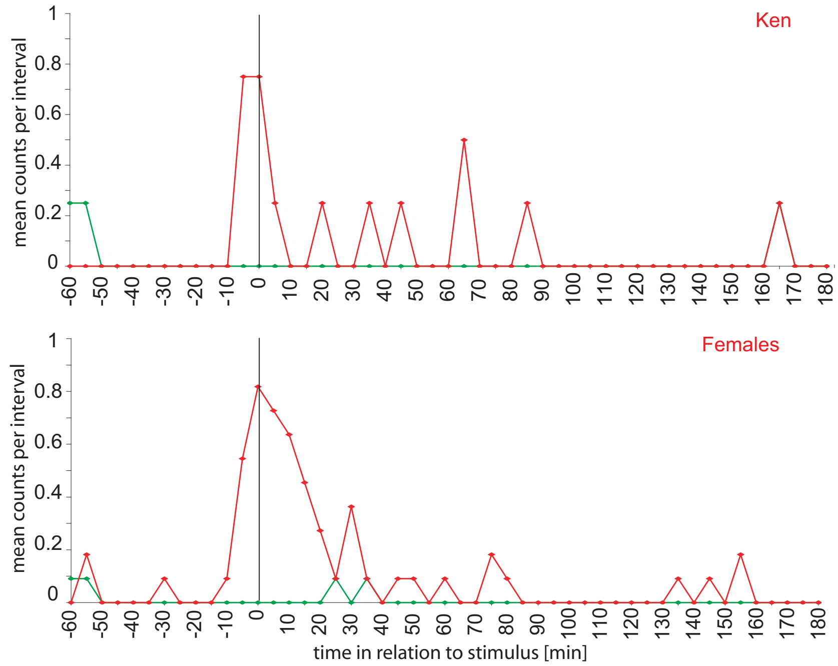

Figure 3.50: Time relation of feeding and locomotor activity to browse removal.
PSTH for catching, weighing and pouch check (in females) during six weeks each in summer and winter for *Ken* and the females (N_{Ken}= 5, $N_{females}$ = 17). 0 indicates the interval the koala is caught and put into a linen bag. The next sample point is the release from the bag, the time the koala is inside the bag (up to 15 minutes) is not shown. Catch up usually took place between 07:00 and 09:00. Green line = feeding, red line = locomotor activity.
Locomotor activity increased in the two intervals before the koala was successfully caught. The koalas settled down within the next hour, but locomotor activity was not very high.

3.6.2 Duisburg

PSTH Morning cleaning and feeding. In the morning, two keepers entered the enclosure several times between 07:40 and 09:30 for cleaning, removal of the old branches and provision of fresh browse. Sometimes there was brief contact with a koala. Usually the door to the keeper's area remained open for most of this time, so the koalas were able to see and hear the koalas in the keeper's area. On some days, *Kambara* tried to leave his enclosure but was immediately stopped by a keeper.

For the PSTH-graphs, three signals have been analysed, the first entering of the keeper, the removal of the old branches and the introduction of the fresh browse. The actual time span between these events differed between days, ranging between minutes to an hour. Therefore, the koala's reaction to an event is reflected in every graph, but at different points of the time-axis.

In *Kambara*, locomotor activity increased about 50 minutes prior to the first entering of the keeper (Fig. 3.51). At this time, the keepers had not entered keeper's area and were not in hearing range of the koalas. No changes were visible when the keeper entered or the old branches were removed. After the fresh browse was introduced, locomotor activity and feeding increased within the next 35 minutes and reached the former level after 90 minutes.

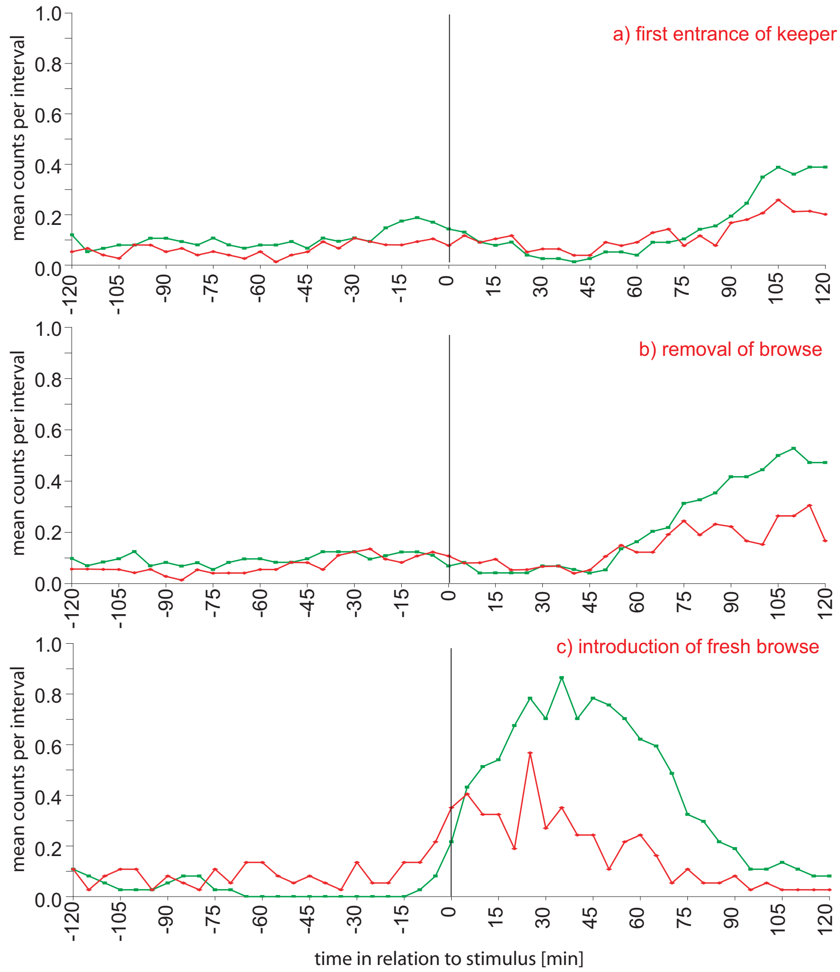

Figure 3.51: Time relation of feeding and locomotor activity to morning husbandry events in Kambara. PSTH for morning husbandry events during six weeks each in summer and winter. (a): 0 indicates the time the keeper entered the enclosure for cleaning and checking the koalas (07:59 ± 20 min). (b): 0 indicates the time the keeper removed the old branches (8:23 ± 18 min). (c): 0 indicates the time fresh browse was introduced (09:42 ± 38 min). Green line = feeding, red line = locomotor activity.
locomotor activity increased about 50 minutes prior to the first entrance of the keeper and remained on that level. Feeding and locomotor activity increased when fresh browse was introduced. Both behaviours reached a low level about 90 minutes after this.

In the females, activity during the morning was very low (Fig. 3.52). This did not change with the keeper's entrance or the removal of browse. Although there was some feeding about 35 minutes prior to the introduction of fresh browse, there was an increase in feeding afterwards (0.23 counts per interval). This was lower than in the male (0.86 counts per interval).

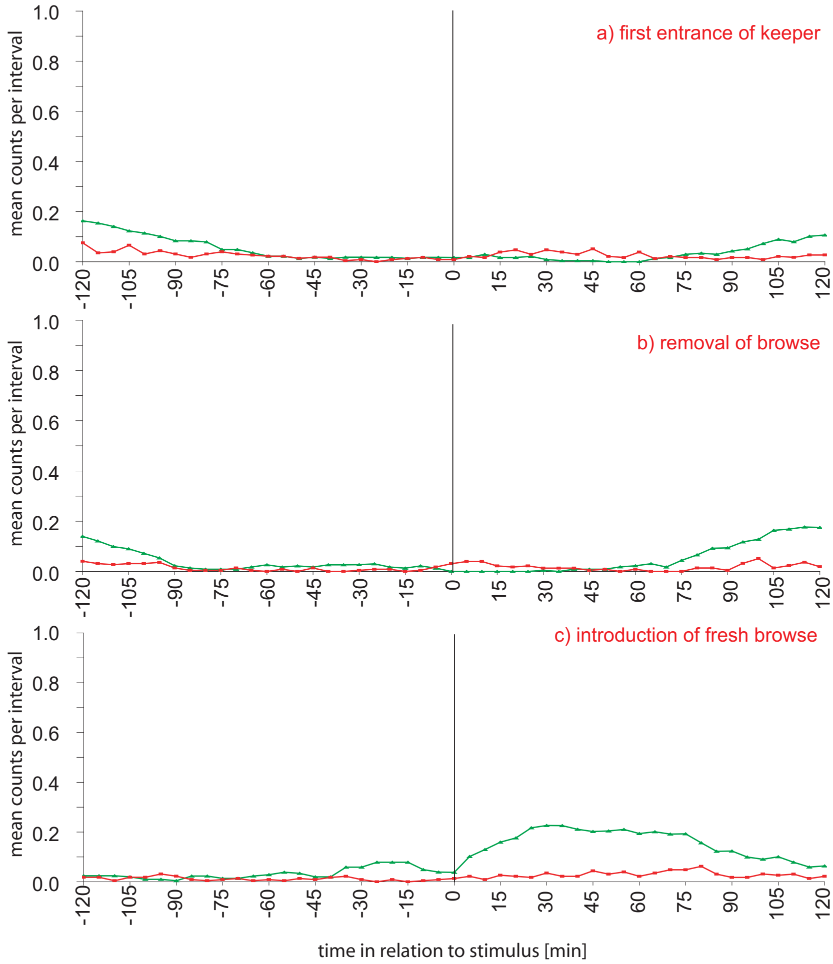

Figure 3.52: Time relation of feeding and locomotor activity to morning husbandry events in the three females.

For details see Fig. 3.51.

There was little activity during the morning, which did not change with the entrance of the keeper and the removal of the browse. Feeding slightly increased 35 minutes prior to the introduction of the fresh browse and increased afterwards. The level at the beginning of the cleaning session was reached after 115 minutes.

Weighing. Twice a week (usually Wednesday and Sunday) the koalas were weighed by the keeper. During observation time, this schedule was varied slightly (see Figs 3.19 to 3.21 for exact dates of weighing).

Kambara usually fed prior to weighing (Fig. 59). Locomotor activity was high in the interval before he was handled. During this time he was able to see the keeper preparing the scale. Feeding commenced immediately after he was returned. The females reduced feeding about 30 minutes prior to weighing. In the intervals prior to and immediately after handling locomotor activity was high. At this time the other females were handled. Within 10 minutes the females settled down and regained feeding.

Figure 3.53: Time relation of feeding and locomotor activity to weighing in *Kambara* and the three females. PSTH for morning husbandry events during six weeks each in summer and winter. 0 indicates the time the individual koala is returned to the fork (11:08 $\pm$ 6 min). Green line = feeding, red line = locomotor activity. *Kambara* was feeding prior to the weighing and started feeding immediately after being returned. There was an increase in locomotor activity in the interval before handling and immediately afterwards. In the females, feeding was already getting reduced in the 30 minutes prior to the weighing, five minutes prior until 15 minutes after the handling locomotor activity was high.

There are no distinct differences between days with weighing and days without in summer (Fig. 3.54). The only exception was *Kangulandai*, who displayed an activity peak between 13:30 and 16:00 on days with weighing, but a peak at 16:00 on days without weighing. All koalas displayed a peak at 10:00, independent whether they were weighed at that time or not. In *Yuri*, this peak was very small. Fresh browse was introduced at 10:00 $\pm$ 37 minutes. This was usually followed by an increase in feeding activity.

3.6.3 Tiergarten Schönbrunn Vienna

PSTH Morning cleaning and feeding. In the morning, the keeper entered the enclosure between 07:00 and 09:30 to clean the enclosure and exchange the browse. The time of the first entering, the removal of the branches and the introduction of fresh browse varied between days and probably interfered with each other in the PSTH.

In *Bilyarra* activity was on a low level before the keeper entered for the first time (Fig. 3.55). Locomotor activity increased slightly when the keeper was inside the enclosure, but was immediately reduced after the fresh browse was introduced, and *Bilyarra* started to feed.

Mirra Li showed low levels of activity 60 to 15 minutes prior to the keeper's first entrance (Fig. 3.56). Locomotor activity started to increase 10 minutes before the keeper entered and reached a peak in the interval after that event, remaining high for 60 minutes. A second peak was reached after the fresh browse was provided, for *Mirra Li* started to feed and locomotor activity decreases.

PSTH weighing. Every day at 10:15 the koalas were removed from the tree and put on a scale with a firmly attached fork. Afterwards the koalas were put back on a tree and fresh browse was introduced by the keeper.

Feeding and locomotor activity at the beginning of the diagram was related to the morning cleaning session. *Bilyarra* rested during the 20 minutes prior to the weighing. After he was returned to the branch, he showed a high peak in locomotor activity in the

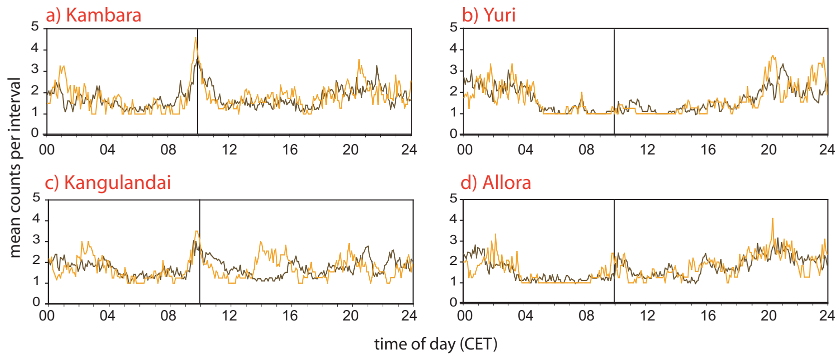

Figure 3.54: Average levels of activity of the Duisburg koalas with and without weighing in summer. Activity profiles (5 minute intervals) averaged from 3 June to 14 July 2003. Black line = days without weighing, orange line = days with weighing. Vertical black line indicates time of weighing.
There were no distinct differences in *Kambara* (a), *Yuri* (b) and *Allora* (d). Only in *Kangulandai* (c) there was a high level of activity between 13:30 and 16:00 on days with weighing, while on days without, activity increases around 16:00. In all koalas an activity peak was visible at 10:00, independent from weighing.

first interval and remained on a high level for the next 40 minutes. He started feeding when fresh browse was provided. After 60 minutes *Bilyarra* rested again.

Mirra Li was active in the two hours prior to the weighing. Immediately after she was returned to the branch, locomotor activity and feeding increased. Her feeding peak was higher than *Bilyarra*'s, but in both koalas activity ceased at the same time. After 60 minutes activity in *Mirra Li* reached a constant low resting level.

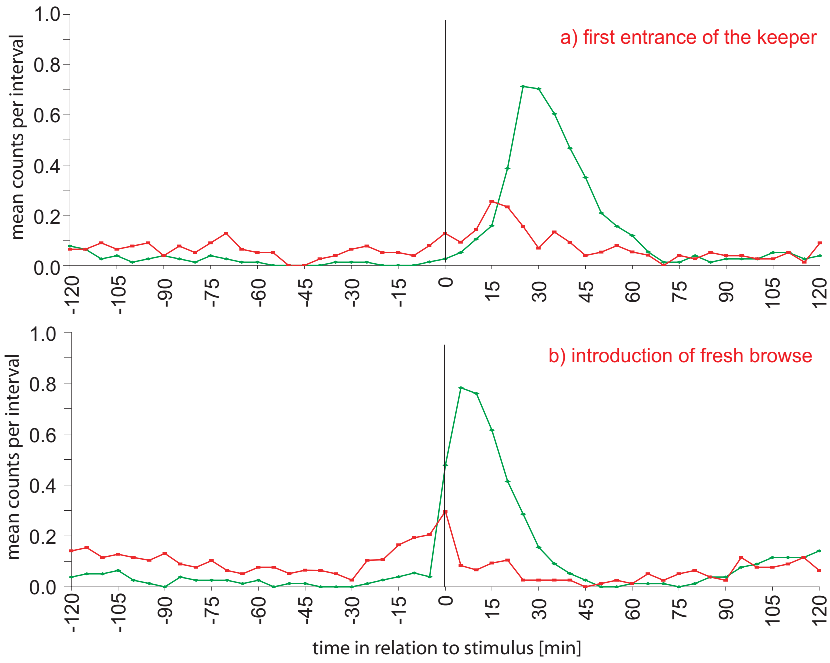

Figure 3.55: Time relation of feeding and locomotor activity to morning husbandry events in *Bilyarra* . PSTH for morning husbandry events during six weeks each in summer and winter. (a): 0 indicates first entering of the keeper (08:14 ± 26 min), including the removal of the old branches. There usually was contact with the koala. (b): 0 indicates the introduction of fresh browse (08:45 ± 32 min). Green line = feeding, red line = locomotor activity.

There was some locomotor activity in the two hours prior to the first entering of the keeper. Locomotor activity increased after the keeper enters. Feeding increased immediately after fresh browse was introduced and locomotor activity was reduced.

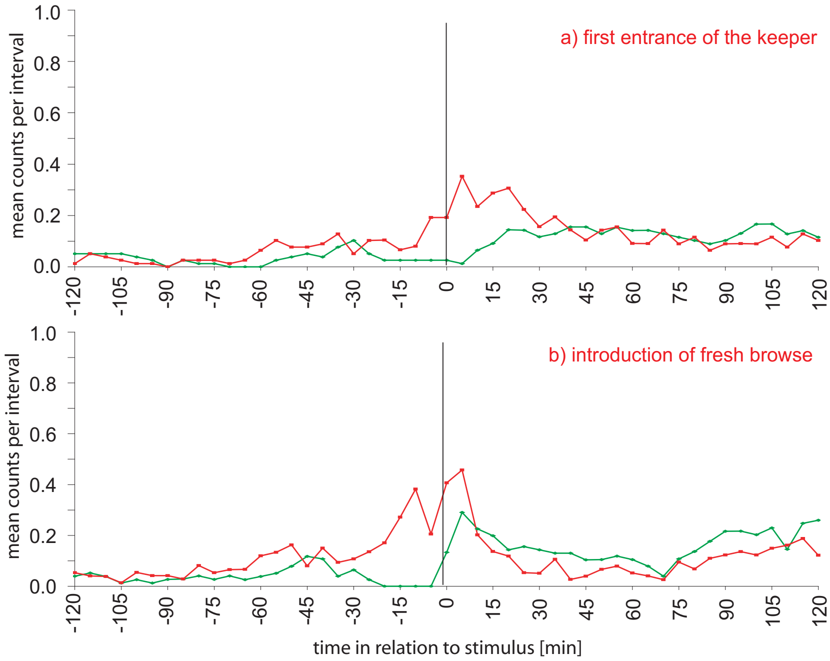

Figure 3.56: Time relation of feeding and locomotor activity to morning husbandry events in Mirra Li. For details see Fig. 3.55.
Locomotor activity started to increase 10 minutes prior to the entering of the keeper and reached a peak in the interval after that event. Feeding increased immediately after fresh browse had been introduced and remained on a medium level for about 60 minutes.

3.6.4 Influence of fixed feeding times

Taronga Zoo: End of Australian Eastern Daylight-Saving Time (AEDT) on 28 March 2004. With the change from Australian Eastern Daylight-Saving Time (AEDT) to Standard time (AEST), the Keeper's Talk had a delay of 60 minutes. On 28 March the old browse was removed at 14:30 standard time which coincidences with the feeding time of the previous weeks.

In *Ken*, no anticipatory activity was observed before 14:30 (Fig. 3.58). Loc2 and Loc3 started after the old browse was removed and *Ken* went to the ground frequently. Locomotor activity ended, after fresh browse was introduced and *Ken* displayed a feeding bout of usual duration. On the second day, locomotor activity began somewhat after 14:30. On day three, *Ken* did not show locomotor activity prior to the Keeper's Talk and feeding started on the following days as soon as fresh browse was provided.

Adori started feeding at 13:40 (Fig. 3.59). The feeding bout was terminated by the keeper, when all browse was removed. Loc2 was observed in three intervals until fresh browse was presented by the keeper, then *Adori* started to feed. Similar to *Ken*, there was some locomotor activity prior to the Keeper's Talk on the next day, then she should

Figure 3.57: Time relation of feeding and locomotor activity to weighing in the Vienna koalas.
PSTH for morning husbandry events during six weeks each in summer and winter. 0 indicates the time the koala is released after the weighing (10:22 $\pm$ 4 min). Shortly afterwards, usually within the next 15 minutes, fresh browse is introduced by the keeper. Green line = feeding, red line = locomotor activity.
After *Bilyarra* was released he mostly showed short locomotor activity. On some days this activity was prolonged, sometimes also he started to feed afterwards. *Mirra Li* mostly fed after she was released, additionally there was some locomotor activity.

patterns as before.

Carrie was feeding when the browse was removed (Fig. 3.60). Feeding started again after fresh browse was presented. Similar to *Ken*, there was locomotor activity on the next day after the browse was removed. From day 4, there was sometimes locomotor activity after the browse had been removed and feeding usually started as soon as the fresh browse was presented.

In *Yindi* the comparable reaction to the keeper's time shift was the weakest, but on the first day after the shift there was also locomotor activity at the old feeding time (Fig. 3.61). Otherwise her locomotor activity was only observed when the old browse was removed. Feeding started after the fresh browse was presented. Little locomotor activity was observed on several of the following days. Feeding started at two occasions: on some days at the Keeper's Talk, on others at dusk, as has been observed in this female throughout the whole year.

On 30 March, three days after the end of daylight savings fresh browse was presented at 14:50, right after the old browse had been removed. *Carrie* and *Adori* started to feed immediately, *Yindi* and *Ken* waited 10 and 15 minutes before approaching the vases.

Legend for Fig. 3.58, 3.59, 3.60 and 3.61: Double-plotted chronoethogram from 14 March to 12 April 2004. Green bars = feeding, olive bars = feeding and Loc2, orange bars = Loc1, red bars = Loc2, black bars = Loc3; black arrows = time shift, green arrow = fresh browse AEDT, red arrow = fresh browse AEST. Background colours: grey = night; yellow = twilight.

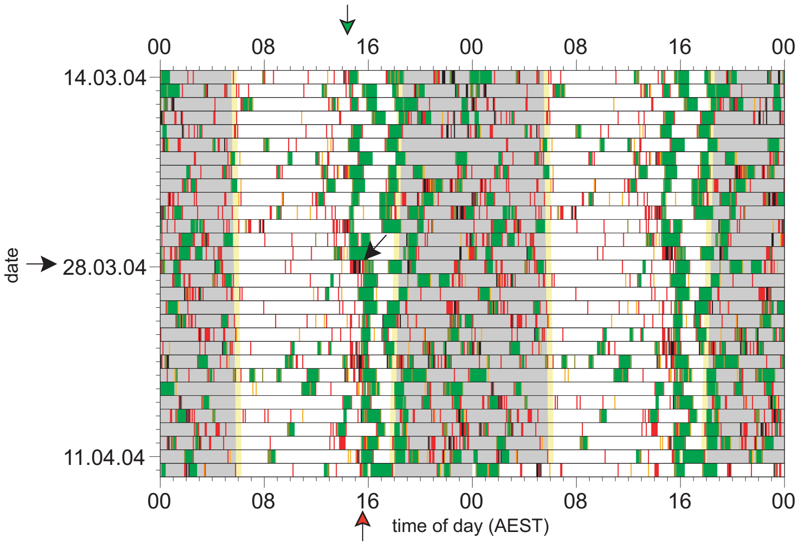

Figure 3.58: Behaviour of *Ken* at the end of Australian Eastern Daylight Saving and the delay of the Keeper's Talk on 28 March 2004.

For details see page 118.

After the old browse had been removed at 14:30, *Ken* started to move around until the fresh browse was introduced. On the next day, there was some Loc2 prior to the Keeper's Talk.

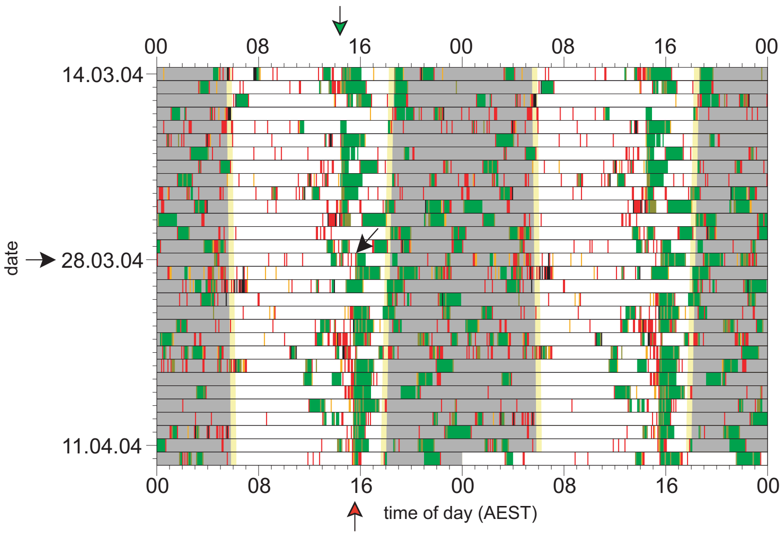

Figure 3.59: Behaviour of *Adori* at the end of Australian Eastern Daylight Saving and the delay of the Keeper's Talk on 28 March 2004.

For details see page 118.

Adori's feeding bout was interrupted by the removal of the browse and after that she showed some locomotor activity until fresh browse was introduced. On day there was some Loc2 prior the Keeper's Talk.

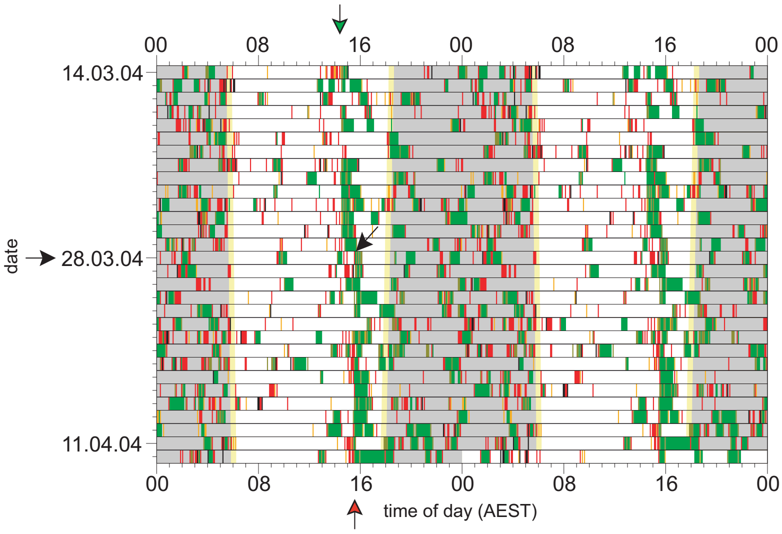

Figure 3.60: Behaviour of *Carrie* at the end of Australian Eastern Daylight Saving and the delay of the Keeper's Talk on 28 March 2004.
For details see page 118.
There was some Loc2 when the old browse was removed and *Carrie* was interrupted in a feeding bout. After this she showed no activity until the fresh browse was introduced and started feeding then. On day 2 there was more locomotor activity prior to the Keeper's Talk.

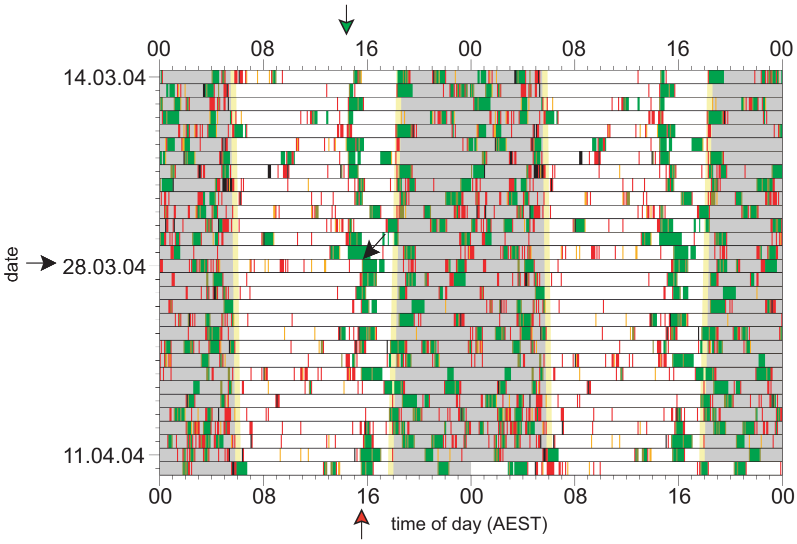

Figure 3.61: Behaviour of *Yindi* at the end of Australian Eastern Daylight Saving and the delay of the Keeper's Talk on 28 March 2004.
For details see page 118.
Yindi showed some short locomotor activity when the old browse was removed, then rested until fresh browse was provided. There was no locomotor activity prior to Keeper's Talk on the following days.

Taronga Zoo: Begin of Australian Eastern Daylight-Saving Time (AEDT) on 31 October 2004. With the beginning of Australian Eastern Daylight-Saving Time, Keeper's Talk occurred with an advance of 60 minutes. The old browse was removed at 13:50, 100 minutes earlier than the Keeper's Talk on the previous day. All koalas reacted with activity after the food had been removed earlier than usual. When fresh browse was presented by the keeper, all koalas moved around for some minutes before settling down to feed.

On the days before, *Ken* did not always start feeding immediately after food had been presented (Fig. 3.62). On 31 October, *Ken* reacted with locomotor activity for two intervals and started feeding in the third interval. A feeding bout of four intervals followed, in which he moved around a lot. On the following days, *Ken* started feeding after fresh browse had been presented.

Adori had started feeding immediately after food had been presented on the days before (Fig. 3.63). On 31 October, a short feeding bout started at 13:30 and locomotor activity was observed after the old browse had been removed. After fresh browse had been presented, she immediately started feeding. On the following days, feeding always started during Keeper's Talk.

In *Carrie*, locomotor activity started when the old browse was removed (Fig. 3.64). She started feeding immediately after the fresh browse had been presented. On the following days she usually showed locomotor activity before 14:30 and started feeding during the Keeper's Talk.

In the time prior to 31 October, *Yindi* started to feed during the Keeper's Talk only on some days, on other days she waited till dusk (Fig. 3.65). When the browse was removed on 31 October, she climbed onto the arm of the keeper and was carried around for several minutes. She also moved around after the keeper left the enclosure. When fresh browse was introduced she immediately started to feed.

Legend for Fig. 3.62, 3.63, 3.64 and 3.65: Double-plotted chronoethogram from 17 October to 14 November 2004. The old browse was removed at 13:50, 100 minutes earlier than on the previous day. Green bars = feeding, olive bars = feeding and Loc2, orange bars = Loc1, red bars = Loc2, black bars = Loc3; black arrows = time shift, green arrow = fresh browse AEDT, red arrow = fresh browse AEST. Background colours: grey = night; yellow = twilight.

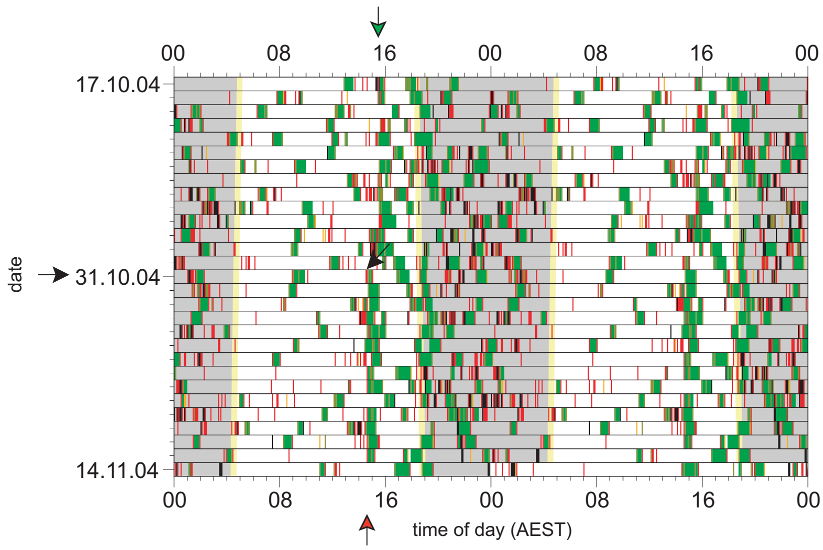

Figure 3.62: Behaviour of *Ken* at the beginning of Australian Eastern Daylight Saving and the delay of the Keeper's Talk on 31 October 2004.

For details see page 121. *Ken* showed no activity after the old browse was removed early and started to feed after the fresh browse had been introduced.

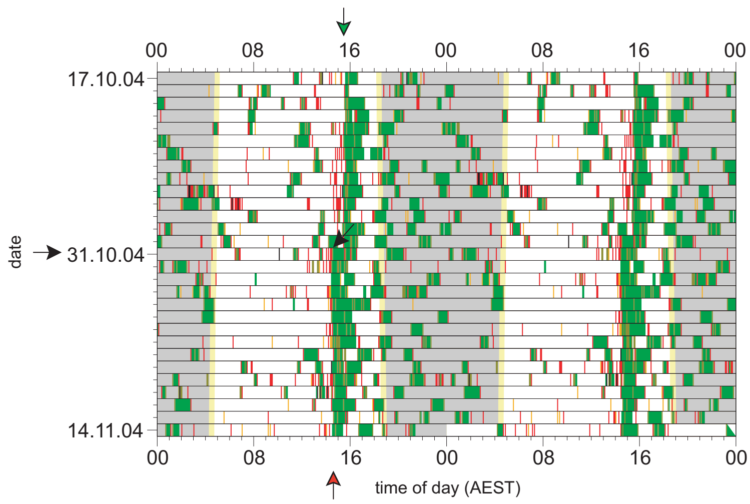

Figure 3.63: Behaviour of *Adori* at the beginning of Australian Eastern Daylight Saving and the delay of the Keeper's Talk on 31 October 2004.

For details see page 121.

Adori showed locomotor activity after the old browse had been removed and started to feed immediately after the fresh browse had been introduced.

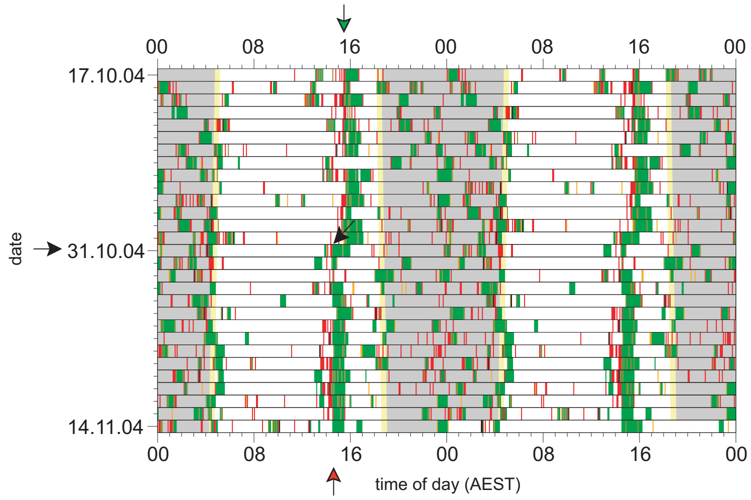

Figure 3.64: Behaviour of *Carrie* at the beginning of Australian Eastern Daylight Saving and the delay of the Keeper's Talk on 31 October 2004.

For details see page 121.

Carrie started to move around after the old browse had been removed and started feeding after the fresh browse was introduced.

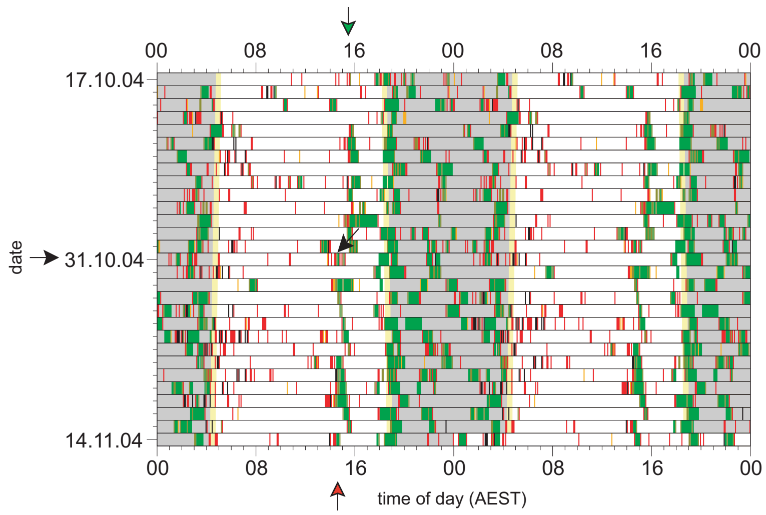

Figure 3.65: Behaviour of *Yindi* at the beginning of Australian Eastern Daylight Saving and the delay of the Keeper's Talk on 31 October 2004.

For details see page 121.

Yindi approached the keeper, when she removed the browse and was carried around by her. After that *Yindi* moved around and started feeding immediately when the fresh had been introduced.

Taronga Zoo: Late feeding on 31 December 2003. On 31 December 2003 the old browse was removed at 13:30, but there was no Keeper's Talk at 14:30. Fresh browse was presented at 17:15.

In *Ken* there was some Loc2 after the browse had been removed (Fig. 3.66a). Starting at 15:15 on, *Ken* moved around more intensely, checking all food vases at 16:20 and the entrance door at 16:35, from which on Loc3 was observed until the fresh browse was brought in. When at 17:10 the door was opened briefly by the keeper, *Ken* waited with *Cooee* in front of the door for a few minutes. *Ken* started feeding immediately after fresh browse was put into the vases.

Adori showed Loc2 at 14:25, 15:15 and 15:25, but not later (Fig. 3.66b). She started feeding 15 minutes after the fresh browse was presented.

In *Cooee* some Loc1 and Loc2 started, after the old browse had been removed (Fig. 3.66c). Loc2 increased after 15:00 and was observed in every interval after 16:40, ending with presentation of the fresh browse. When at 17:10 the door was opened briefly, *Cooee* waited with *Ken* in front of the door. *Cooee* started feeding immediately after the browse was put into the vases, but moved around for 15 minutes before finally settling down.

Felicity showed little Loc2 between the removal of the old and presentation of the fresh browse but started feeding immediately after the browse was put into the vases (Fig. 3.66d).

In *Yindi* there was no locomotor activity after the old browse was removed (Fig. 3.66e). *Yindi* climbed onto the dead trees on top of the vases while the food was put into the vases, and stayed there until 17:50 before climbing down to feed. At this time *Cooee* had just stopped feeding.

Legend for Fig. 3.66.: Double-plotted chronoethogram from 26 December 2003 to 5 January 2004. The old browse was removed at 13:30, but no Keeper's Talk took place at 14:30. Fresh browse was introduced at 17:15. Green bars = feeding, olive bars = F & L, orange bars = Loc1, red bars = Loc2, black bars = Loc3; black arrows = time shift, green arrow = fresh browse AEDT, red arrow = fresh browse AEST. Background colours: grey = night; yellow = twilight.

Ken (a) and *Cooee* (c) moved around after the old browse had been removed until the fresh browse was introduced. Then both started to feed. *Adori* (b) and *Felicity* showed no anticipatory behaviour. *Felicity* started immediately after the fresh browse had been introduced, *Adori* began 15 min later. *Yindi* (e) showed no activity at all and did not start to feed before 17:50.

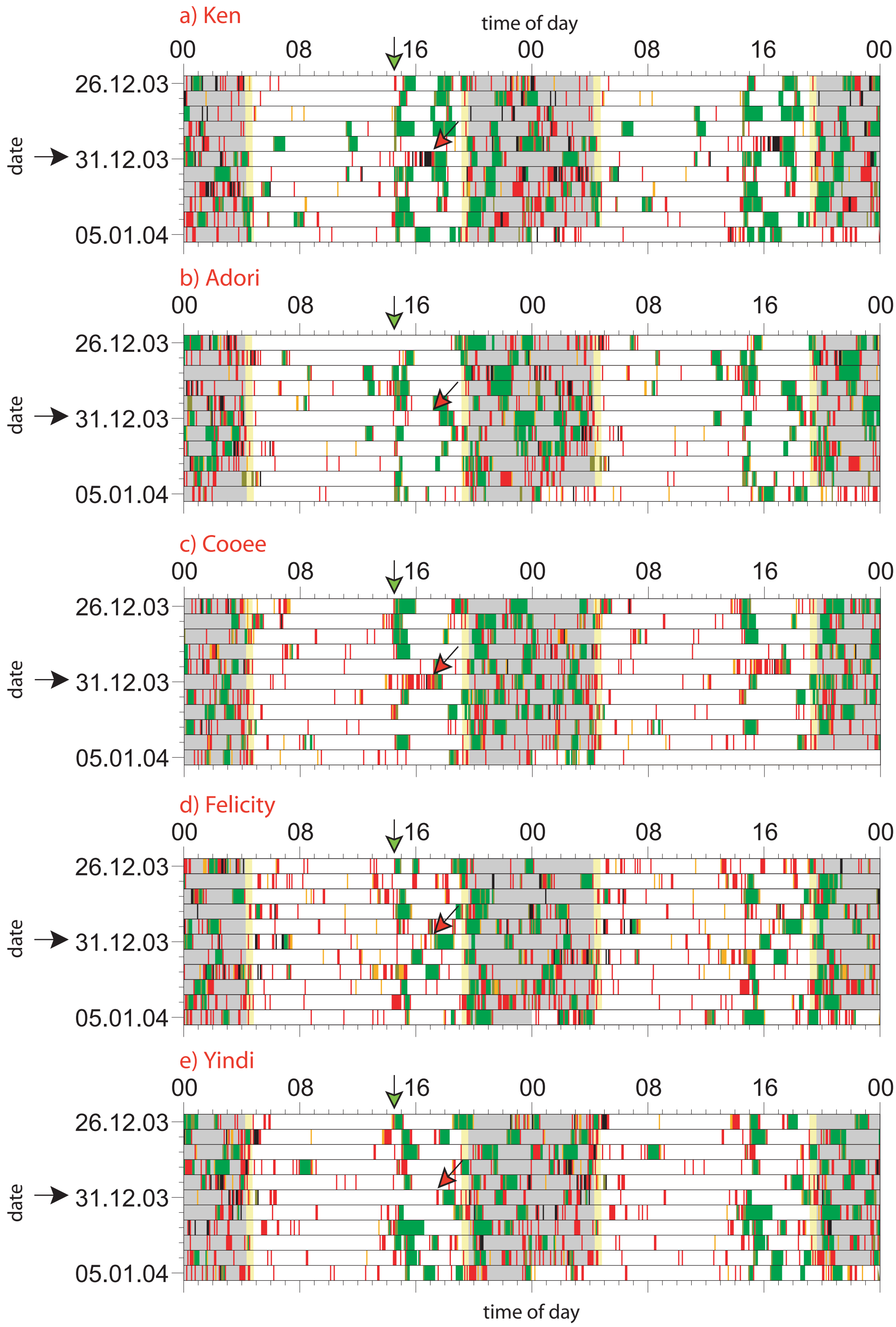

Figure 3.66: Behavioral pattern for the Sydney koalas on 31 January 2004, when feeding time was delayed by 3 hours.

For details see page 124.

Vienna Zoo: Change of feeding/weighing times. The chronoethograms show that all koalas at Koala Walkabout and some at Duisburg Zoo rested during the morning. At Vienna Zoo, both koalas were handled daily at 10:15, but usually rested prior and after handling. To assess whether such handling acts as Zeitgeber or masking factor, weighing and feeding time were shifted from 10:15 to 16:00 on 01 June 2005.

In the two weeks prior to the shift, the ethogram of *Bilyarra* shows a small band of locomotor activity at 10:15, resulting from a change of location after weighing (Fig. 3.67a). This is also obvious in the activity profile as a high peak (Fig. 3.68a). There was no activity prior and after the weighing. This band abruptly ends on 01 June, when the male was not handled at 10:15. From this day on, little activity was seen between 10:00 and 14:00 (also see Fig. 3.68c,e). During the complete observation, there were feeding bouts in the afternoon. From 01 June a small, straight band of locomotor activity and feeding was visible in between these bouts at 16:00. There were also two peaks in the activity profile (Fig. 3.68c,e). In the first week after the shift, weighing was followed by a high peak in locomotor activity and a lower peak in feeding. After two weeks, locomotor activity was lower and was followed by a feeding bout.

In the female, there were only little changes visible. The chronoethogram shows activity bouts distributed over the complete 24 hours (Fig. 3.67b). Weighing was followed by some locomotor activity and feeding, but this activity bout was not longer than those during the remaining time. The bout was followed by a longer resting period. In the afternoon, frequent feeding and locomotor activity had been observed between resting periods. After the weighing time had been shifted to the afternoon, there were still

Legend for Fig. 3.67.: Double-plotted chronoethograms from 18 May to 28 June 2004. Shift of weighing time from 10:15 to 16:00 on 01 May. Height of column indicates relative level of activity. Green columns = feeding, red columns = locomotor activity; blue arrow = morning cleaning, yellow arrow = old weighing time (10:15), blue arrow = new weighing time (16:00). Background colours: grey = night, yellow = twilight.

In the two weeks prior to the time shift of weighing there was a clear line of locomotor activity in *Bilyarra*. It lasted for one period and there was no activity before and after the weighing. The line immediately disappeared on 01 May, and now weighing was frequently followed by feeding. *Bilyarra* now rested between 10:00 and 13:00. In *Mirra Li* there was a band of locomotor activity and feeding after the weighing, but it disappeared between regular activity bouts. After 01 May, feeding became more common after the weighing but resting periods in the morning were not prolonged.

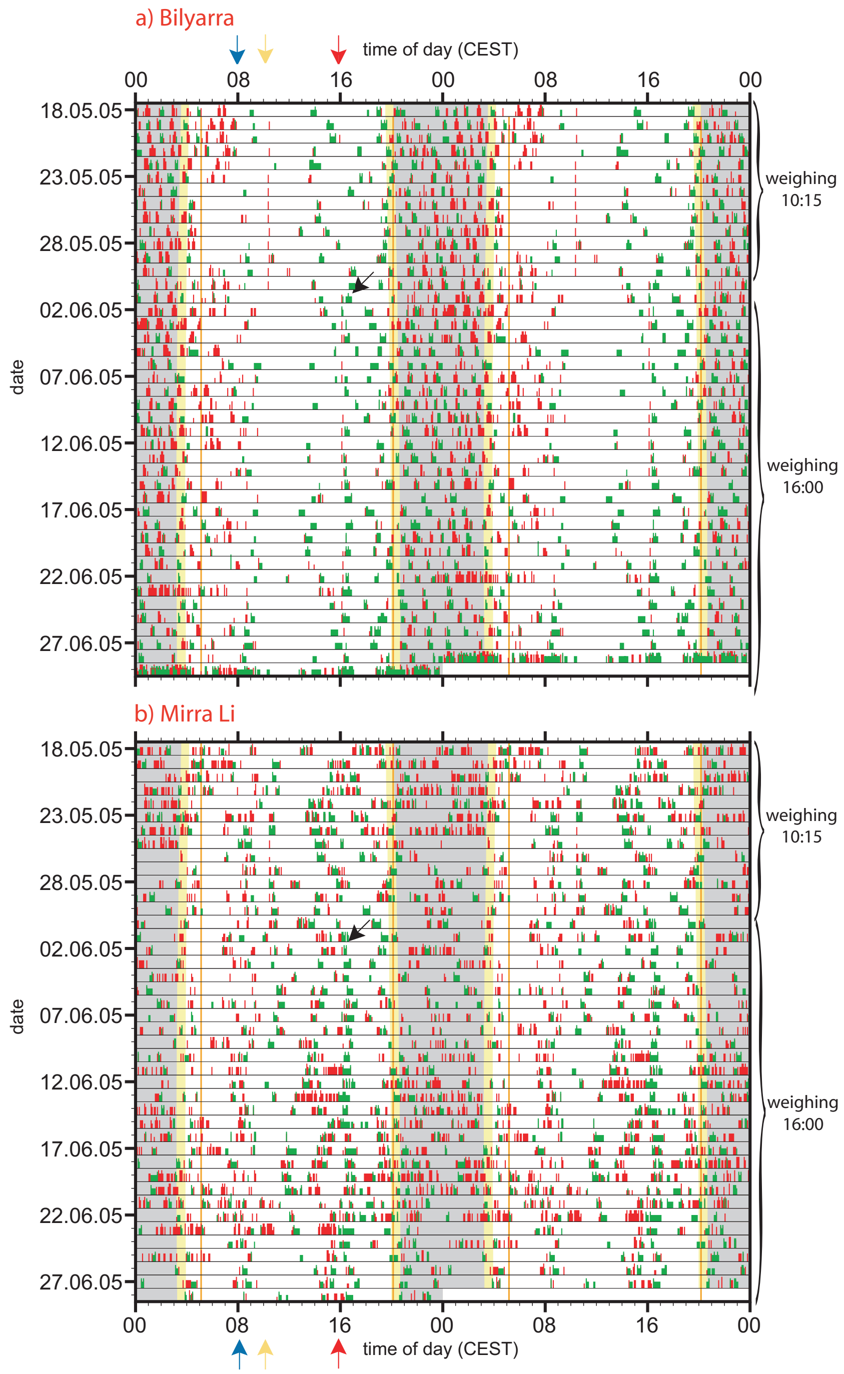

Figure 3.67: Total activity in *Bilyarra* and *Mirra Li* during the shift of feeding and weighing time. For further details see page 126.

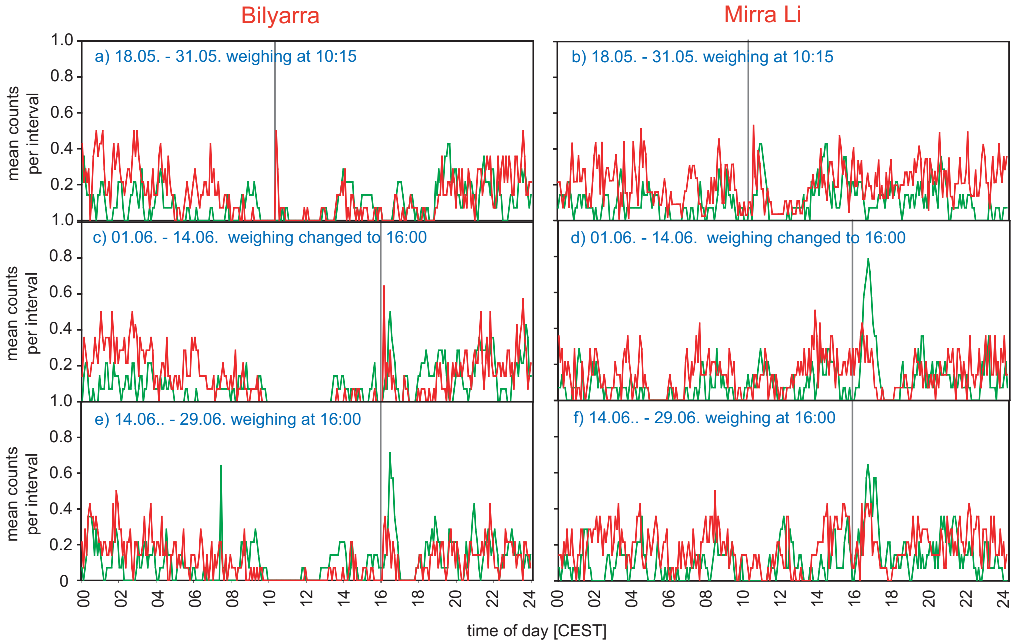

Figure 3.68: Average levels of feeding and locomotor activity prior and after the change of weighing times. Activity profile (5 minute intervals) averaged over two weeks each. Vertical black line indicates time of weighing. Green line = feeding, red line = locomotor activity.

feeding bouts and locomotor activity in the morning. These bouts became less frequent after 10 June, but there still was no prolonged resting period in the morning as had been observed in other koalas and the Vienna male (also see Fig. 3.68c,e). The introduction of fresh browse after the weighing at 16:00 was followed by a band of feeding. This was clearly visible as a peak in the activity profile (Fig. 3.68d,f). Different to the morning peak, this one was well between other locomotion bouts.

In *Bilyarra*, feeding and locomotor activity was more common during the night, but there still was activity during daytime. There was a clear locomotor activity peak at 10:15, but no activity slightly before and little activity afterwards. After the weighing had been changed to the 16:00, there was little activity between 10:00 and 13:00 and a clear feeding peak at 16:00. In *Mirra Li*, activity was high throughout the day. At 10:15 there was a relatively low peak. After the weighing time had been changed, there is a clear feeding peak at 16:30, which became lower in week five and six.

3.7 The influence of visitors: Sydney Koala Encounter (Taronga Zoo)

In addition to the keeper, koalas might be influenced by visitors, especially if they enter the enclosure. The koalas at Koala Encounter (Taronga Zoo) are used two hours daily for photo sessions, in which visitors are positioned next to the koala on its perch. Contact is not allowed.

3.7.1 Reference-chronoethograms

The two females at Bay B, *Carla* and *Maggie*, showed no clear day-night pattern (Fig. 3.69). Activity at night was generally higher than during the day, but there were three peaks in the day. At these times, a keeper routinely was inside the enclosure to control the browse and introduced fresh browse if necessary. This was the case at the beginning of the every visitor sessions (grey boxes). For most of these sessions *Maggie* rested. There was slightly less activity in the afternoon, but resting was regularly interrupted by feeding and locomotor activity. The chronoethogram of *Carla* is similar to that of *Maggie*, but she was generally less active (Appendix A).

The koalas at Bay C, *Georgie* (Fig. 3.70), *Cooee* and the juvenile *Coco* had a more distinct day-night pattern, with more activity, especially locomotor activity during the night. Resting was more common during the day than in Bay B, but again three peaks are clearly visible, related to the introduction of the fresh browse, for example at the beginning of the visitor session. The band at the morning cleaning / feeding time was the clearest. The introduction of the fresh browse at the beginning of the visitor sessions did not happen every day and the koala did not show a daily feeding bout at this time. The chronoethograms of *Cooee* and *Coco* show differences, especially in locomotor activity, which will be discussed in more detail below.

Resting. Again most of the time was spent resting and the ethograms were mirror image to total activity. Therefore, resting is not discussed in detail here.

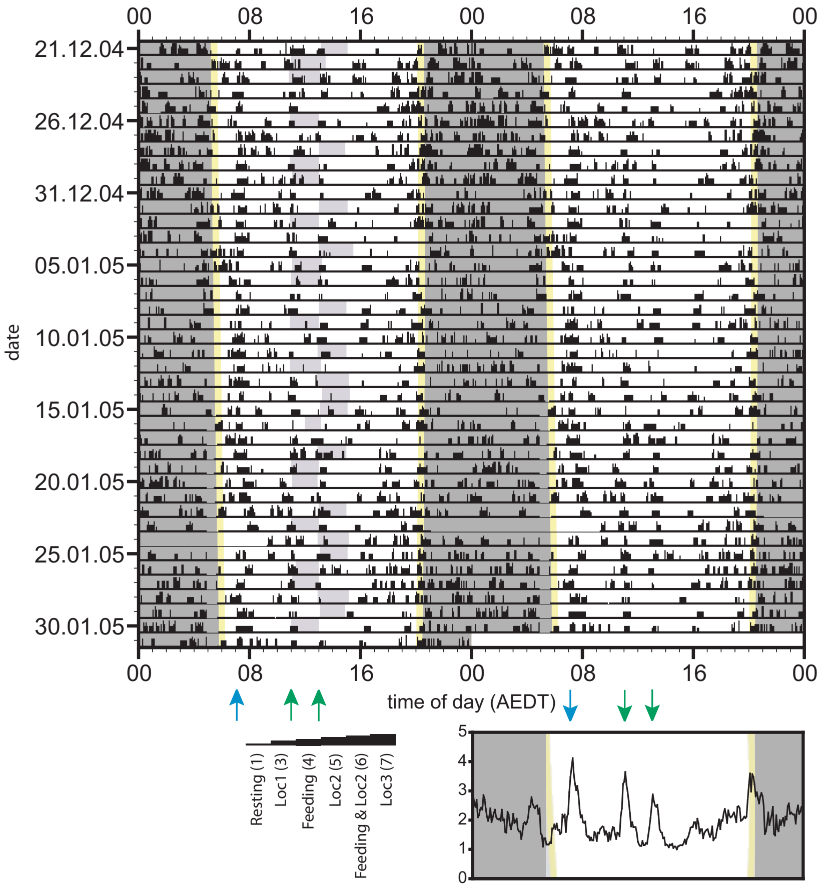

Figure 3.69: Total activity for the female *Maggie* (Bay B) in Southern summer.

Upper panel: double-plotted chronoethogram from 21 December 2004 to 31 January 2005. Height of columns in chronoethogram indicates level of activity. Lower panel: (left) amplitude code of the plotted behaviours, (right) single-plotted activity profile (5 minute intervals) averaged over the complete observation period, same time scale as ethogram above. Background colours: grey = night, yellow = twilight, blue-grey boxes = visitor session. Blue arrow = morning cleaning and first feeding, green arrows = feeding at beginning of visitor sessions.

There was no clear day-night pattern, but the activity profile shows three peaks during the day, related to the introduction of fresh browse. Between the peaks activity was lower during the day than during the night.

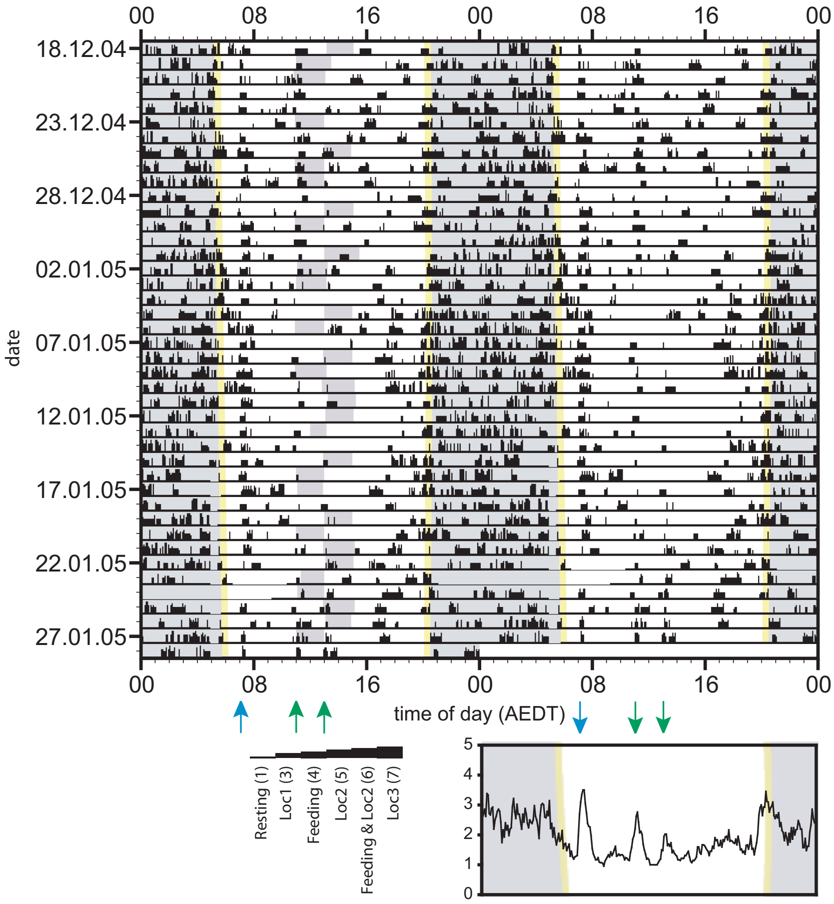

Figure 3.70: Total activity for the female *Georgie* (Bay C) in Southern summer.

Upper panel: double-plotted chronoethogram from 18 December 2004 to 28 January 2005. For further details see Fig. 3.69.

Activity levels were generally higher during the night. Increase and decrease of activity was closely related to sunrise and sunset. During the day there were three peaks related to the introduction of fresh browse.

Feeding. Feeding was the main activity at Koala Encounter and bouts have been observed over the complete 24 hours. There are four bands visible for *Maggie* (Fig. 3.71) one at 07:00, when the keeper entered for the first time to exchange browse and clean the enclosure, at 11:00 and 13:00, when fresh browse was introduced at the beginning of the visitor session, and at dusk. In Bay C, the first peak was as clear as for *Maggie*, but the second peak was much weaker (Fig. 3.71). The third peak is only visible because there is little feeding between the peaks. The peak at dusk was broader than for *Maggie* and began slightly earlier. In Bay C, more feeding was observed at night than in Bay B. For *Maggie*, there was a feeding band at dawn in the first half of the chronoethogram.

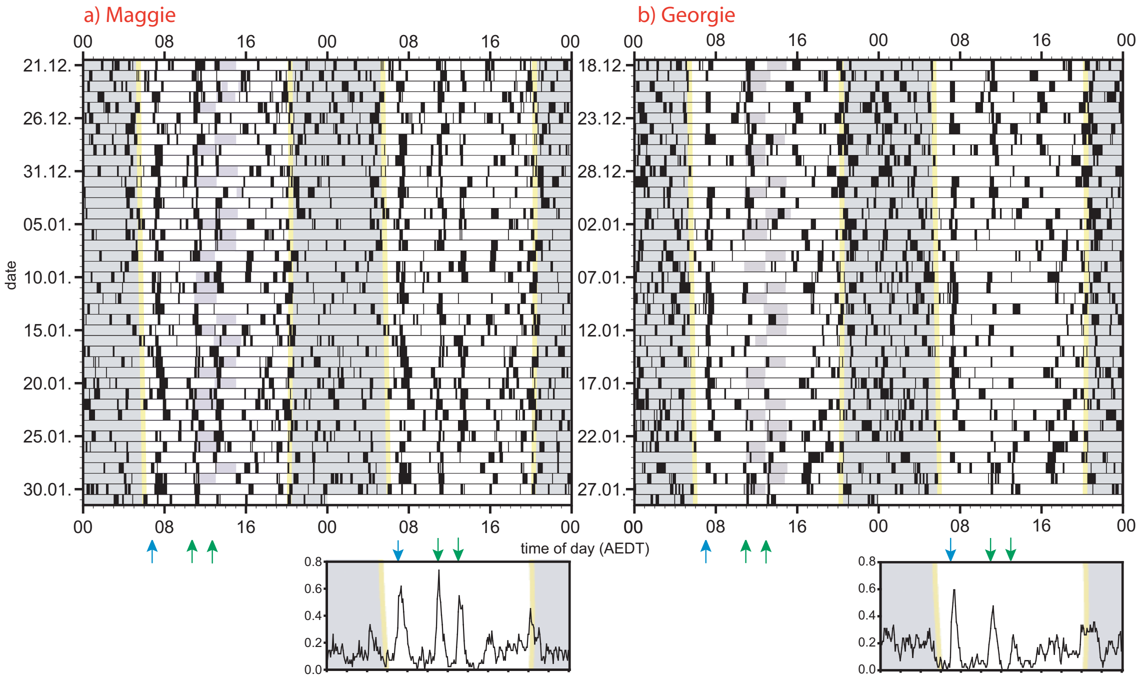

Figure 3.71: Feeding for the females *Maggie* (Bay B) and *Georgie* (Bay C) in Southern summer.
Upper panel: double-plotted chronoethograms from 21 December 2004 to 31 January 2005 of *Maggie* (a) respectively 18 December 2004 to 28 January 2005 of *Georgie* (b). Black bars indicate feeding. Lower panel: single-plotted activity profiles (5 minute intervals) averaged over the complete observation period, same time scale as ethogram above. Background colours: grey = night; yellow = twilight; blue-grey boxes = visitor session. Blue = morning cleaning and first feeding; green arrow = feeding at beginning of visitor sessions.
There were three bands in *Maggie*, related to introduction of fresh browse. These bands were also visible in *Georgie* also, but the latter two were not as pronounced as in *Maggie*. In *Maggie* there were also bands at dusk and before dawn in the first part of the chronoethogram. The dawn band was also visible in *Georgie*, but at dawn feeding ended without another band.

Locomotion. In all koalas, locomotor activity was more common during the night. In *Georgie*, this day-night pattern was stronger than in *Maggie* (Fig. 3.72b). There were few, short locomotion bouts during daytime. Between 07:00 and 08:00, the usual time for morning cleaning, there was a band of locomotor activity. The activity profile showed two small peaks at 11:00 and 13:00 which were not visible as bands in the chronoethogram. Locomotor activity had a high peak at dusk and remained on a high level during the night. On most days there was no locomotor activity between sunrise and morning cleaning. In *Maggie*, the difference between day and night was not as clear in the chronoethogram, but she had a high peak at dusk too, and locomotion levels were higher during the night. locomotor activity remained high in the morning. The activity profile showed a peak at 07:00, but the band was not as clear, since there were many locomotion bouts before noon.

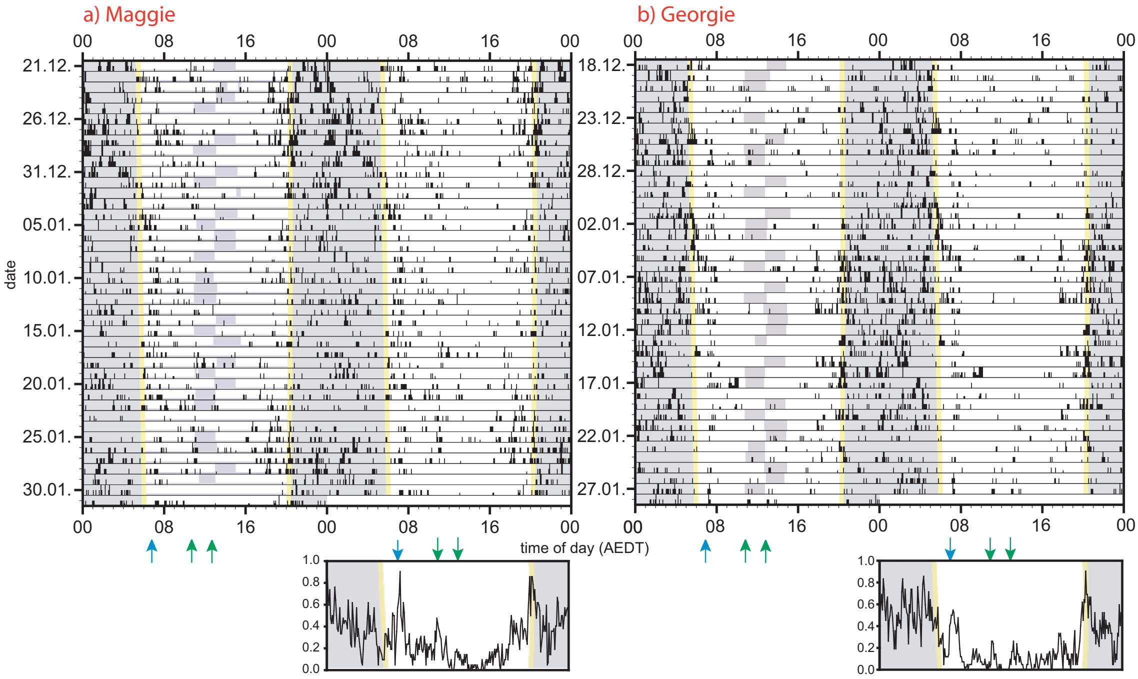

Figure 3.72: Locomotor activity for the females *Maggie* (Bay B) and *Georgie* (Bay C) in Southern summer. Upper panel: Height of the black columns indicates the level of locomotor activity (Loc1, Loc2, Loc3). For further details see Fig. 3.71.
Locomotor activity was more common during the night. This pattern was clearer in *Georgie*. Both koalas had a peak during the morning cleaning and two smaller one at 11:00 and 13:00. This peaks were not clearly seen as bands in the chronoethogram. In *Maggie*, locomotor activity increased in the late afternoon, in *Georgie* this was not as strong. Both koalas had one period with increased levels of locomotion, *Maggie* within the first two weeks of observation, *Georgie* between 05 and 16 January.

In the afternoon, locomotor activity was not as common. Both koalas had periods with increased locomotor activity. The same was true for the other three koalas and in some koalas this happened at the same time (B.3).

On ground. The koalas came to the ground regularly to change trees or explore the enclosure. Feeding and resting was not observed on the ground. Generally the koalas at Koala Encounter spent more time on the ground during the night (Fig. 3.73).The activity profiles show that this increase was related to sunset and sunrise, but there were days when a koala came to the ground shortly before sunset or shortly after sunrise. As in locomotor activity there were periods when a koala came to the ground more often. These periods correlate with the periods of increased locomotor activity.

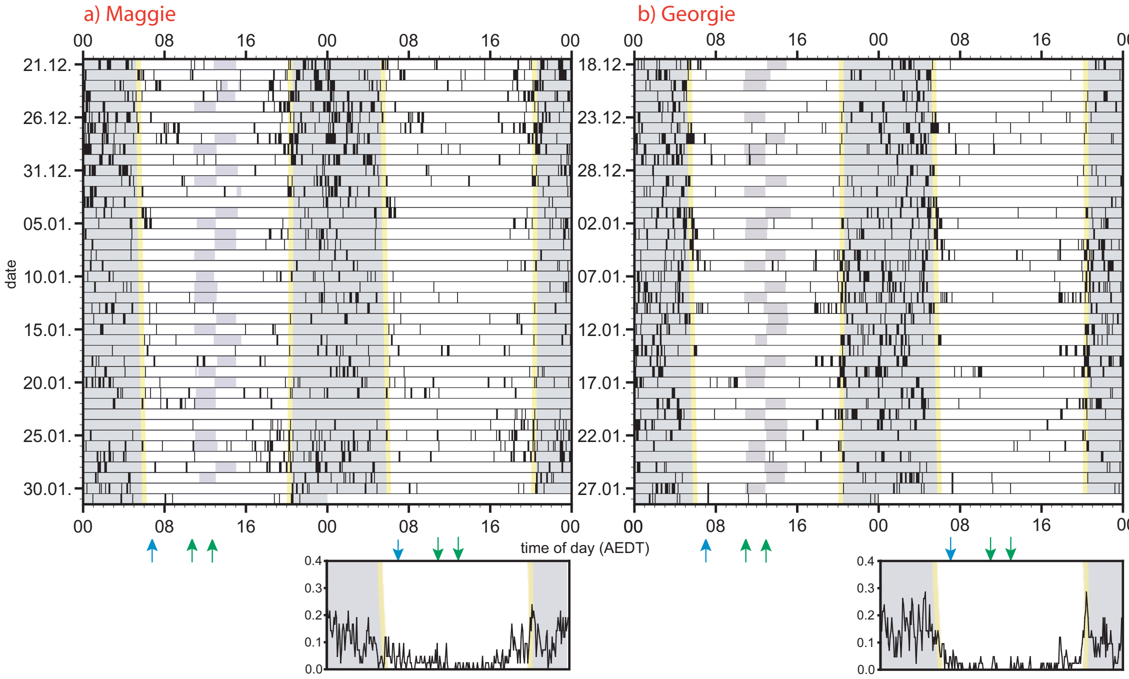

Figure 3.73: Presence on ground in *Maggie* (Bay B) and *Georgie* (Bay C).
Upper panel: black bars indicate presence on ground. For further details see Fig. 3.71.
Both koalas were more often on the ground during the night. The activity profile shows the close relation to sunset and sunrise. In *Georgie* the difference between day and night is bigger than in *Maggie*. There were periods in which a koala came to the ground more often and these periods corresponded to those of increased activity.

3.7.2 Comparison to Koala Walkabout

A comparison of the chronoethograms of Koala Encounter and Koala Walkabout shows that the patterns during the nights were very similar in both enclosures (Fig. 3.75). The nightly peak in feeding and locomotor activity was at dusk, between 20:00 and 21:00. Activity had the lowest values between 02:00 and 02:30, and there was another small peak shortly before sunrise. One difference was a peak in locomotor activity around midnight at Koala Encounter, while locomotion levels were low during this time at Koala Walkabout.

The patterns during the day, however, differed dramatically. In both enclosures, there was a peak when fresh browse was introduced. At Koala Encounter there were three short peaks at 07:00, 11:00 and 13:00 with little activity in between. The Walkabout koalas rested during this time, but locomotor activity increased after 14:00. At 15:30 browse was introduced; feeding activity peaked and remained high until 18:00. At Koala Encounter, feeding was observed in the late afternoon too, but there was no external stimulus. Loco-

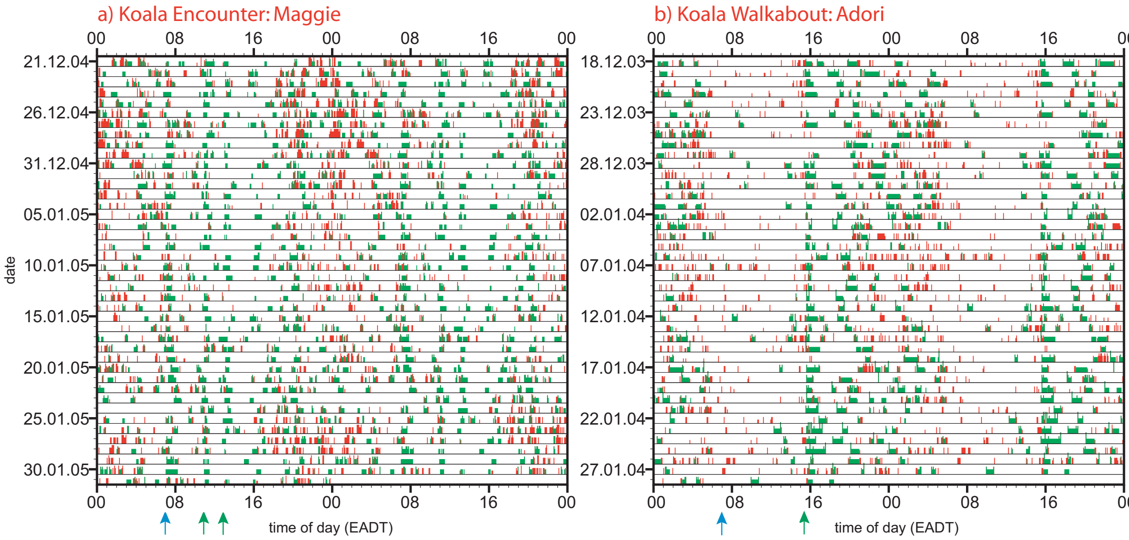

Figure 3.74: Total activity for Koala Encounter (Maggie) and Koala Walkabout (Adori).
Double-plotted chronoethogram from six weeks each in summer of *Maggie* (a) and *Aori* (b); height of column indicates relative level of activity. Green columns = feeding, red columns = locomotor activity; blue arrow = morning cleaning and first feeding, green arrows = Encounter - feeding at beginning of visitor sessions / Walkabout - feeding at Keeper's Talk. Background colours: grey = night, yellow = twilight.
At Koala Encounter activity had been observed throughout the complete 24 hours, also there were three bands of activity during the day. At Koala Walkabout little activity had been observed during the morning and there was only one band of activity in the afternoon.

motor activity was more common at Koala Encounter in the afternoon and early evening than at Koala Walkabout.

Differences have also been found in time budget and day:night ratios. The koalas at Koala Encounter rested significantly less than those at Koala Walkabout (Fig. 3.76). They fed longer and showed significantly more locomotor activity. Loc2 was more than five and Loc3 more than three times as high as in Koala Walkabout.

The koalas at Koala Encounter rested slightly more during the day than those at Koala Walkabout (Fig. 3.77). Day:night ratios for feeding and locomotor activity on the other hand were more negative at Koala Walkabout. For Loc3 (intensive locomotor activity) and presence on ground the difference was significant. The biggest difference in ratios was in feeding. At Koala Encounter feeding was equally distributed between day and night with little more feeding at night time. At Koala Walkabout there was significantly more feeding during the night. This was caused by the two additional feeding peaks seen in the activity profile at Koala Encounter (Fig. 3.75a)

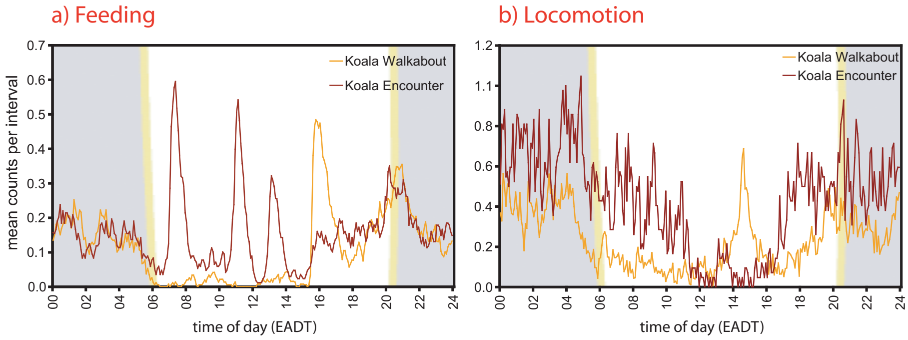

Figure 3.75: Average levels of feeding and locomotor activity for Koala Encounter and Koala Walkabout.
Activity profile (5 minute intervals) averaged over 42 days each in summer 2004/05 at Koala Encounter and in summer 2003/04 at Koala Walkabout (females' values only). Background colours: grey = night; yellow = twilight. Brown line = Koala Encounter (N = 4), orange line = Koala Walkabout (N = 4).
The patterns of feeding and locomotor activity in both enclosures at night were similar, but there was a striking difference in the diurnal peaks: at Koala Walkabout there was one peak at 15:30, beginning with the Keeper's Talk; at Koala Encounter there were three peaks, each one related to introduction of fresh browse.

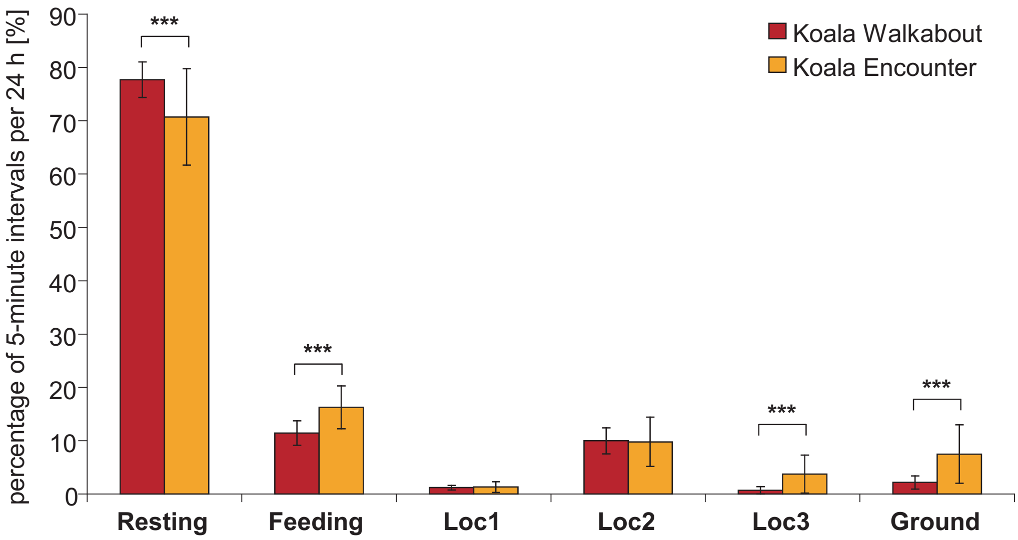

Figure 3.76: Average time budget of females for different behaviours at Koala Walkabout and Koala Encounter.
Percentage of 5 min observation intervals per 24 hours during 42 days; mean values for four females at each enclosure over six weeks. Bars indicate standard deviation between individuals. Feeding and Loc2 have been regularly observed in one interval. In this case, the interval was counted for both behaviours, so the sum of all behaviour is bigger than 100%. Presence on ground is counted independently. Asterisks indicate significant differences between koalas, *** $p < 0.001$.
Koalas at Koala Encounter rested significantly less than at Koala Walkabout. Also they spend significantly more time with feeding and Loc3 (intensive locomotor activity) and came to the ground more often.

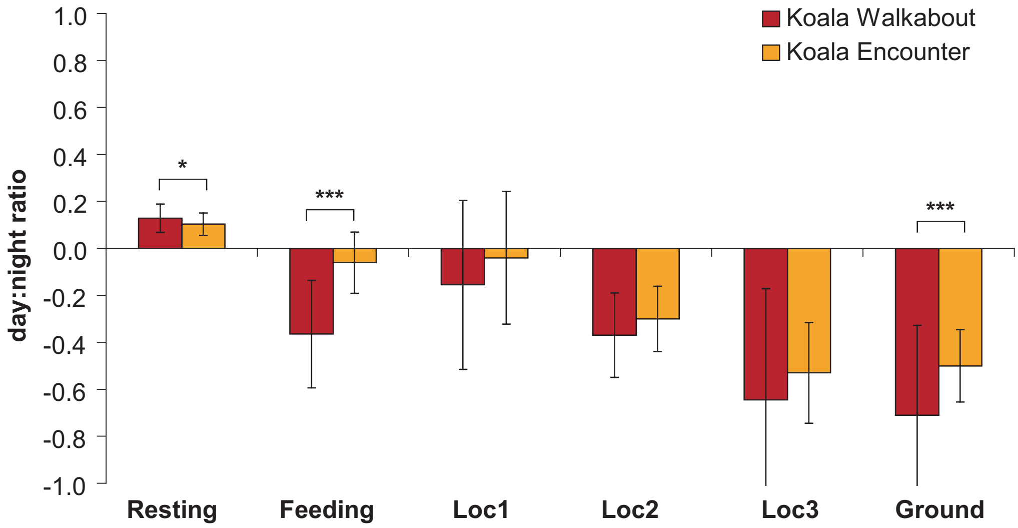

Figure 3.77: Average day:night ratio of females for different behaviours at Koala Walkabout and Koala Encounter.

Positive values indicate that behaviour was more often observed during the day, negative value that is was more often observed during the night; mean values for four females at each enclosure over six weeks. Bars indicate standard deviation between days. Asterisks indicate significant differences between groups, * $p < 0.05$, *** $p < 0.001$. For further details see details Fig. 3.76.

The koalas at Koala Walkabout rested slightly more during the day. Loc3 and presence on ground had very similar ratios in both enclosures, but were significantly more common during the night at Koala Walkabout than at Koala Encounter. The biggest difference in ratio was in feeding: the koalas at Koala Encounter feed more often during daytime than those at Koala Walkabout.

3.7.3 Feeding bouts

The koalas at Koala Encounter had on average 12.4 ± 3.32 feeding bouts per day. This was twice as high as at Koala Walkabout, where the females had a mean number of feeding bouts of 6.4 ± 2.01. The mean length of a feeding bout was 21.24 minutes, which is significantly shorter than the 31.08 minutes at Koala Walkabout.

The histogram shows similarities with Koala Walkabout (Fig. 3.78), but longer feeding bouts were slightly rarer and the longest observed feeding bout lasted 100 minutes. This is shorter than the longest bouts observed in the females at Koala Walkabout at the same time.

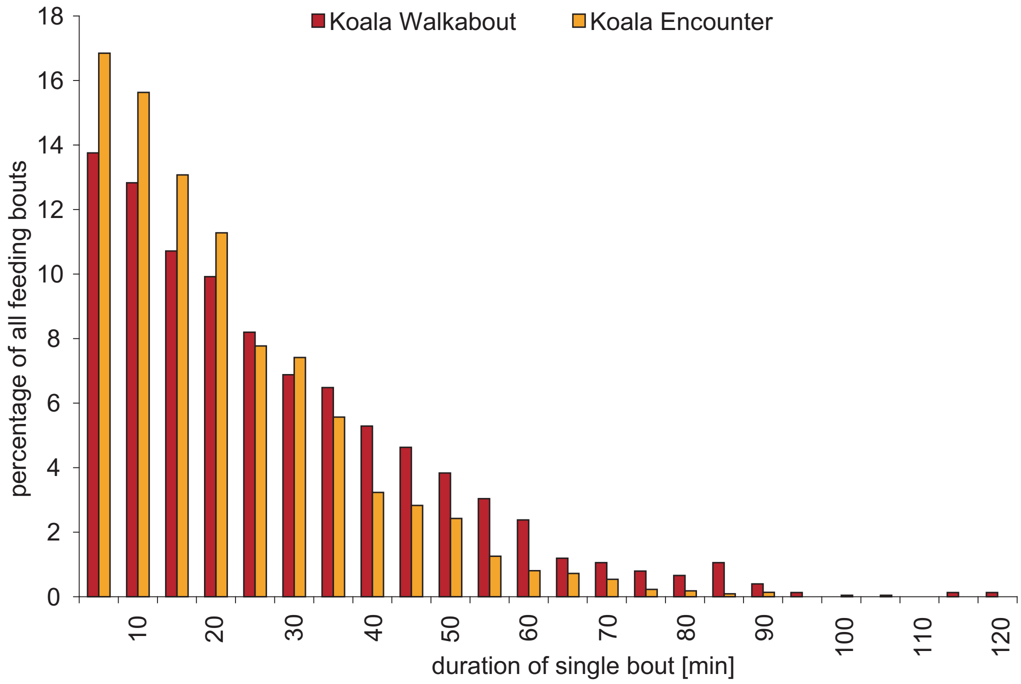

Figure 3.78: Duration of single feeding bouts for Koala Walkabout and Koala Encounter. Histogram calculated of all feeding bouts observed during six weeks in Southern summer (December-January).Values of four females each enclosure (subadult *Coco* excluded). Number of observed feeding bouts $N_{Koala-Walkabout}$= 707, $N_{Koala-Encounter}$= 2006. Short bouts are more common at Koala Encounter, median, mean and maximum duration are smaller.

3.7.4 External influences

Influence of the keeper. The keeper usually entered the enclosure three times a day. The first occasion was around 07:00, when two keepers partly removed and rearranged the old browse, introduced fresh branches and cleaned the enclosure. Often the koalas were verbally addressed and in the case of *Maggie* and *Carla* sometimes touched. During the keeper's work, the koalas sometimes changed their location. The normal schedule was to clean Bay C first, then continued to Bay B and A, so the koalas at Bay B usually saw the keeper before she entered.

The second occasion was around 11:00, prior to the first visitor session. Additional browse was introduced and on some days the photographer prepared their equipment for the session. In that case, visitors entered at 11:00 and stayed for two hours (see below). The same happened at 13:00 at the beginning of the second visitor session, but fresh browse was only introduced on some days.

At all three times, there was an increase in feeding after the fresh browse was introduced, as well as a small increase in locomotor activity. (Fig. 3.79). The highest increase was at 07:00, when all individuals started to feed and fed for a longer period of time. This can also be seen as a clear band in the chronoethograms. At 11:00 and 13:00 the PSTH still shows an increase in feeding, but it is lower than at 07:00. *Maggie* and *Carla* had a high increase in feeding at 11:00, but this was not the case at Bay C, where feeding started to increase only 15 to 25 minutes after the fresh browse had been introduced. Additional browse was not added daily at 13:00, but all koalas had an increase in feeding at this time, especially those at Bay B. Locomotor activity only slightly increased when browse was introduced. No anticipatory behaviour was observed.

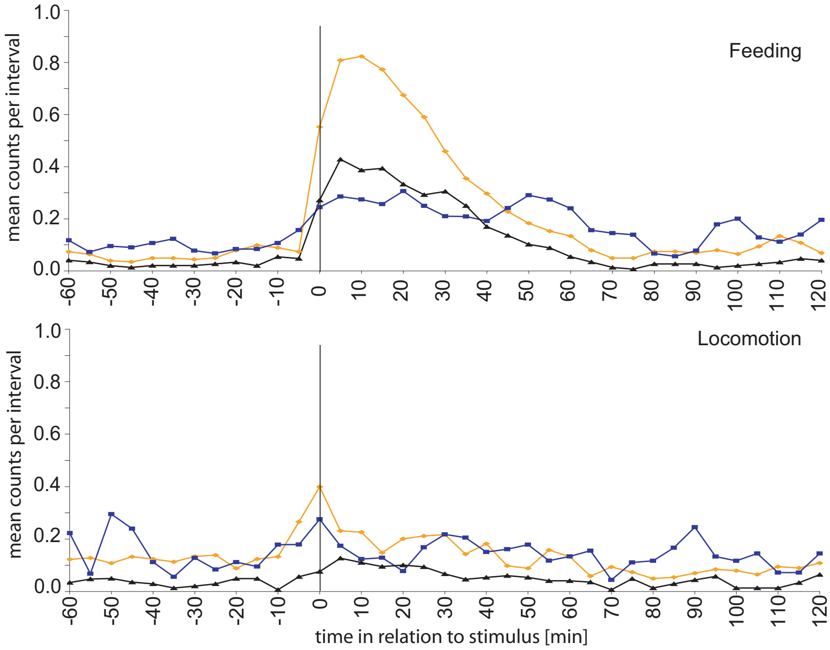

Figure 3.79: Time relation of feeding and locomotor activity to the introduction of fresh browse.
PSTH for the introduction of fresh browse over six weeks in summer and winter each for *Ken* and the females (N_{sum}= 4, N_{win}= 2). 0 indicates the introduction of fresh browse. Orange line = morning cleaning session (07:08 $\pm$ 14 min), Blue line = second feeding (10:50 $\pm$ 7 min), black line = third feeding (12:57 $\pm$ 8 min, fresh browse on every day).
Feeding increased immediately after the fresh browse was presented. However, the first peak (07:00) was the highest, the other two peaks were lower. Locomotor activity increased slightly before the browse was presented, probably due to the keeper's presence.

Influence of visitors on time budget. Behaviour between 11:00 and 13:00 (session 1) and 13:00 and 15:00 (session 2) was compared during the visitor's session and on days without visitors (Fig. 3.80). Independent from the presence of visitors, the koalas rested for more than 79.8% to 85.0% of the time. Resting was slightly higher if visitors were

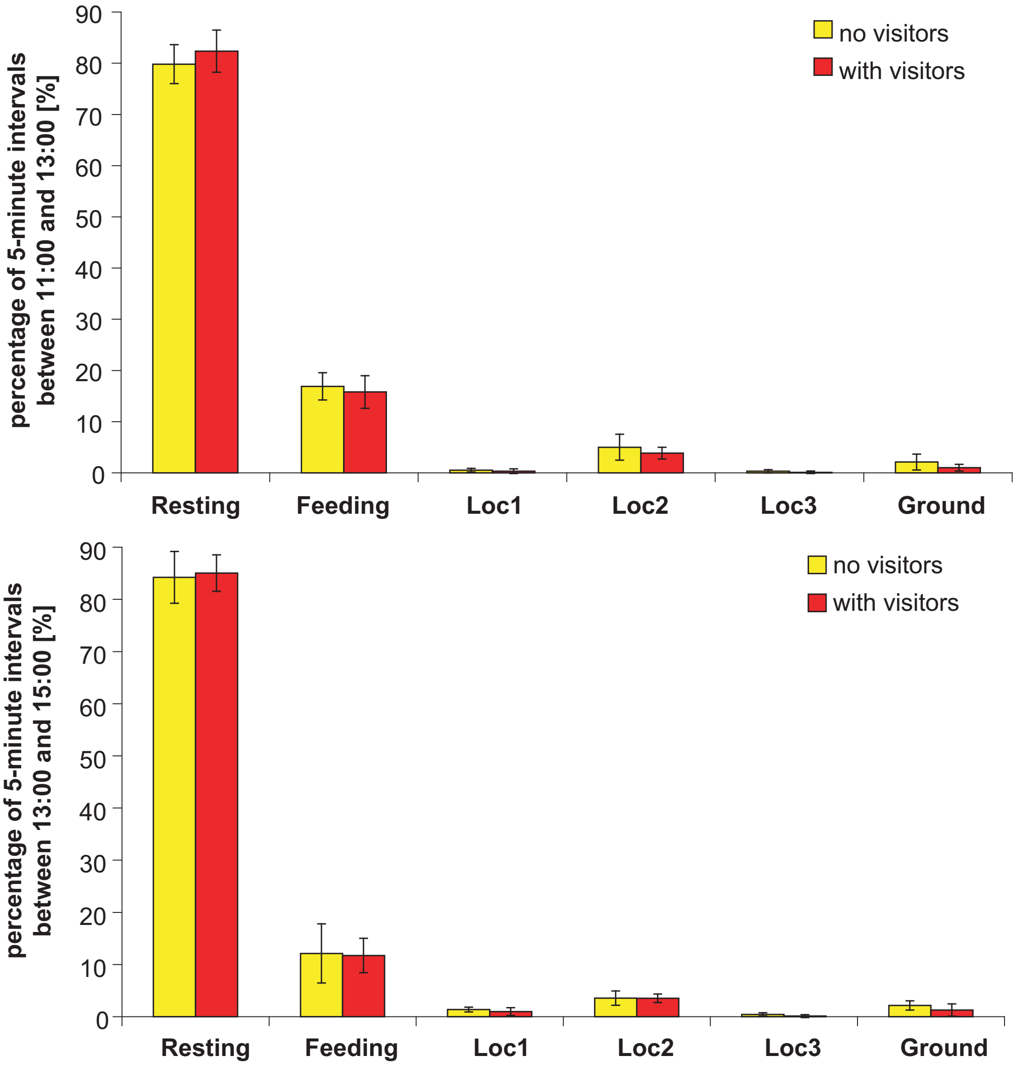

Figure 3.80: Average time budget for every behaviour with and without visitors during session time. Percentage of observation intervals during (upper panel) 11:00 to 13:00 (visitor session 1) and (lower panel) 13:00 to 15:00 (visitor session 2); mean values for 4 females over 11 days, bars indicate standard deviation between individuals. Values without visitors were obtained on days without visitor sessions. Feeding and Loc2 have been regularly observed in one interval. In this case, the interval was counted for both behaviours, so the sum of all behaviour is bigger than 100%. Presence on ground is counted independently.
There are no significant differences between the two hour intervals on days with or without visitors.

in the enclosure, but the difference was not significant. There also were no significant differences in the other behavioural categories.

If behaviour of the 24 hours following the visitor session is compared, the koalas rest slightly, but not significantly more on visitor days (Fig. 3.81). Loc2 was significantly, Loc3 slightly more frequent on days without visitors.

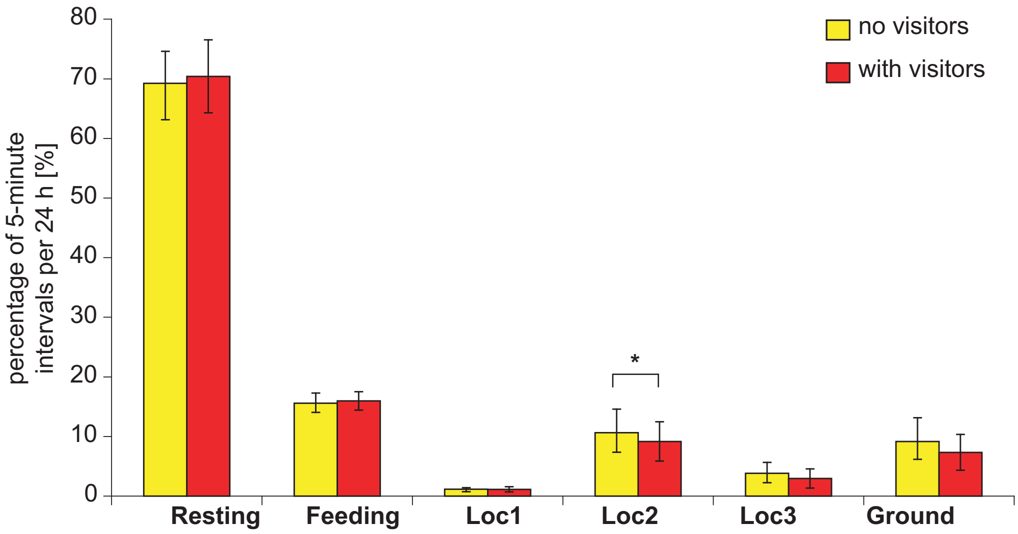

Figure 3.81: Average time budget for every behaviour with and without visitors for the complete 24 hours. Percentage of 5 min observation intervals per 24 hours. Mean values for four females over 11 days. Bars indicate standard deviation between days. Asterisks indicate significant differences between groups, * $p < 0.05$. Fur further details see Fig. 86.
Significant differences have only been observed in Loc2, but not in the other behaviours.

3.7.5 Changes in behaviour: Locomotor activity

During the six weeks of observation Loc2 and Loc3 changed their pattern and their frequency. These changes often occurred in two koalas at the same time.

In *Cooee* and her 13 month old daughter *Coco* there was an increase in locomotor activity between 12 and 22 January, especially in Loc3 (Fig. 3.82). Both koalas went to the ground more often during this time too. In the first three weeks, *Cooee* and *Coco* mostly moved at different times. Now, *Coco* often followed her mother and tried to suckle or ride on her back. So, both koalas moved around at the same time. In some cases the koalas squabbled with each other.

Changes in locomotor activity were also observed in *Maggie* and *Carla* (Fig. 3.83). On 20 December the female *Carla* was transferred to Bay B in exchange for another female and her joey. For *Maggie*, Loc3 was reduced again after 5 January, in *Carla* a first reduction

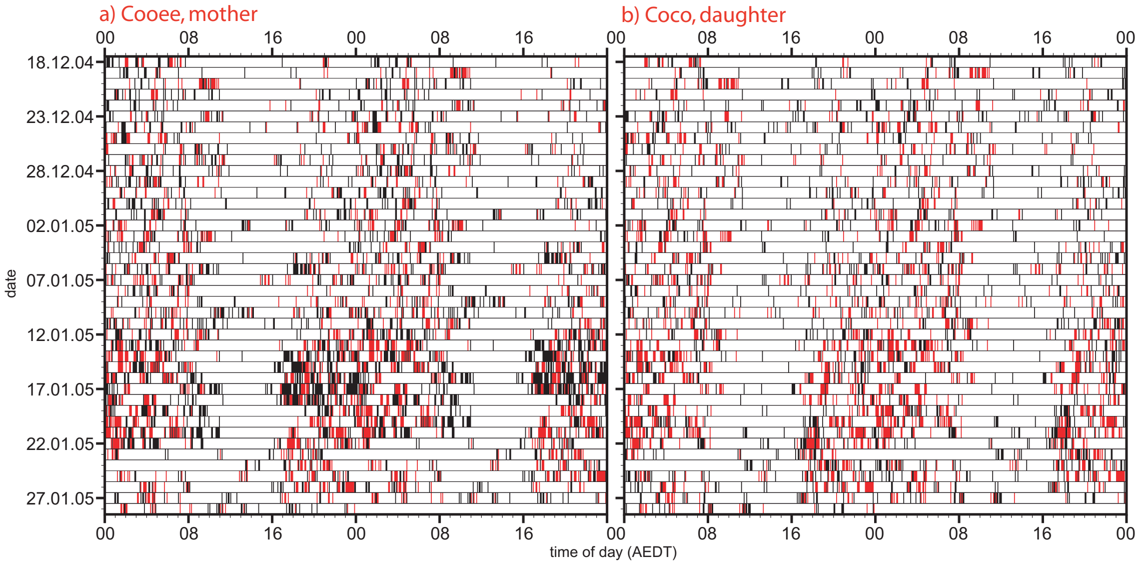

Figure 3.82: Loc2 and Loc3 for *Cooee* and *Coco* from 18 December 2004 to 28 January 2005. Double-plotted chronoethograms from 18 December 2004 to 28 January 2005 of *Cooee* (a) and her daughter *Coco* (b). Black bars = locomotor activity, red bars = locomotor activity in both koalas simultaneously.
At the beginning of the observation both koalas moved around at different times mostly. Between 12 and 22 January Loc2 and Loc3 was increased in both koalas. Especially in *Coco* this behaviour is most often shown simultaneously with the mother *Cooee*.

was seen after 30 December, and after 10 January Loc3 became very rare. Both koalas were observed on the ground more often in the first two weeks of observation. This was more obvious in *Maggie* than in *Carla*. In *Maggie* there was a second increase in Loc3 after 26 January until the end of the observation. This increase was not found in *Carla*.

Georgie showed an increase in locomotor activity, especially in Loc3 between 7 and 17 January (Fig. fig:KE-LOKb). She also went to the ground more often during this time. This increase was not reflected in *Cooee* or *Coco*.

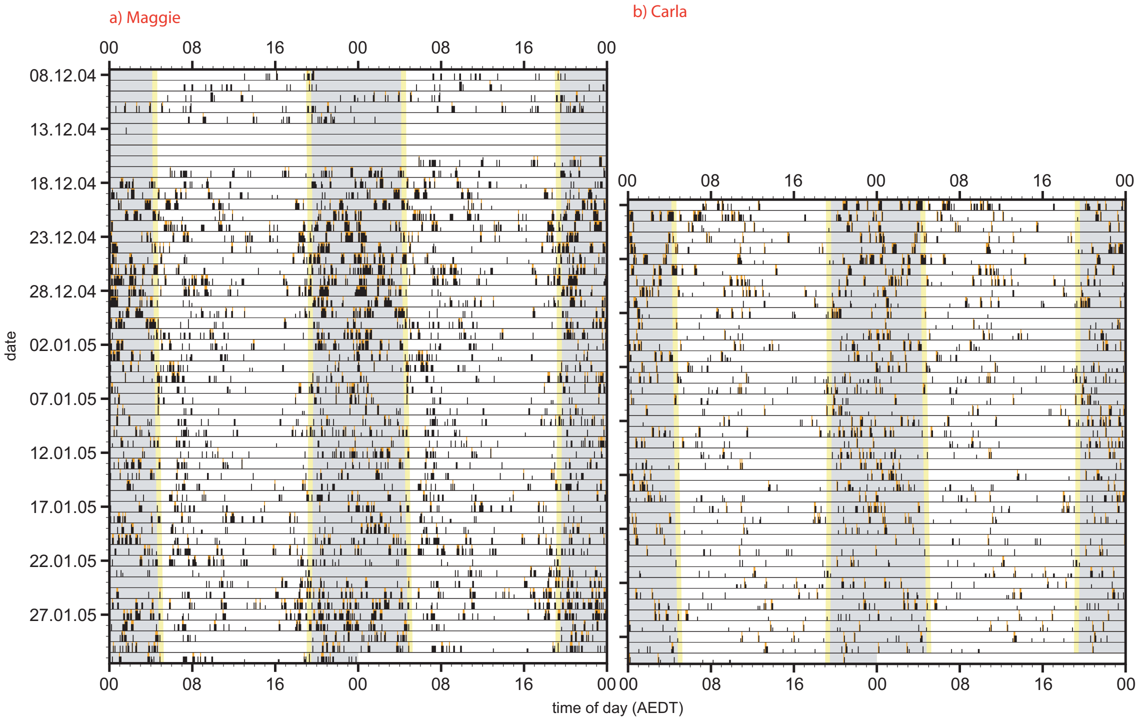

Figure 3.83: Locomotor activity and presence on ground in *Carla* and *Maggie* from 8 December 2004 to 31 January 2005.

Double-plotted chronoethograms from 18 December 2004 to 31 January 2005 of *Maggie* (a) and from 20 December to 31 January 2005 of *Carla* (b); height of columns indicate level of activity. Black bars = locomotor activity, orange bars= presence on ground.

3.8 Social behaviour at Koala Walkabout

Although some social behaviour has been observed, interactions between the koalas were rather rare. The adult koalas showed little interactions. Regularly a koala would move away if approached by another koala. Furthermore chasing has been observed several times, especially a female chasing *Ken*. Unfortunately, it was not always possible to distinguish chasing from a simple approached for three reasons:

- koalas moved away before contact was established,
- physical attacks as biting or scratching were not detectable on video,
- no vocalization was recorded.

Therefore chasing was not analysed quantitatively but counted as avoidance behaviour. Avoidance behaviour was seen regularly. For the time between 11 July and 06 December 04 a total of 700 occasions of avoidance behaviour have been quantitatively

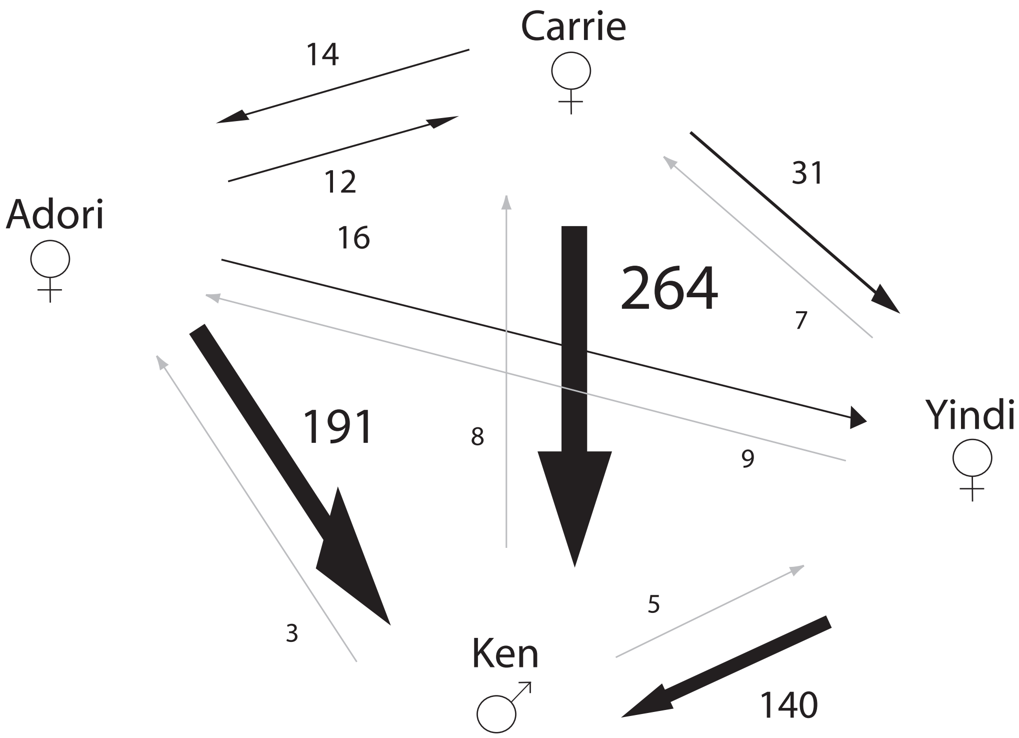

Figure 3.84: Social relationships for Koala Walkabout from 11 July to 6 December 2004.
Diagram indicates avoidance behaviour. Arrow strength and numbers indicate frequency of avoidance behaviour, arrows points from actor to receiver. Total number of observations N = 700.
The male *Ken* clearly had the Ω-position. *Carrie* was the α-animal, but the females' values were close together.

analysed (Fig. 3.84). 85.0% of all avoidance behaviour was observed from *Ken*, moving away most often from *Carrie* (44.4%), then from *Adori* (32.1%) and least often from *Yindi* (23.5%). On the other side he was the koala less often avoided (2.3% of all avoidance), most often by *Carrie* (29.6%), then by *Adori* (11.5%) and less often by *Yindi* (9.6%). *Yindi* has been the female that showed avoidance most often. *Carrie* and *Adori* were equal in avoiding the other koalas, most often each other (*Adori* 53.8%, *Carrie* 44.4%).

3.9 Location

At Koala Walkabout and at Duisburg Zoo, living non-food trees were provided for the koalas. The resting time spent in these locations was analysed to gain information about the importance of these places.

3.9.1 Taronga Zoo

At Koala Walkabout a living non-food tree was available to the koalas. For analysis, this tree was divided into the canopy and the branches without leaves.

In winter, the females spent more than 50 % of their resting time in the canopy, making it the preferred resting location (Fig. 3.85). *Ken* on the other hand spent more than 90% of his resting time on one of the dead trees. The trunk itself was used only little for resting. The chronoethogram shows that for most of the day at least one female was present in the canopy (Fig. 3.86b). At night the canopy was not used as often. *Ken* came into the canopy only for short periods, usually during the night, often without settling down (Fig. 3.86a). Only on rare occasions he was observed there for a longer period (e.g. 09 December). In summer, the dead trees were the preferred resting location of all koalas. The canopy was also used frequently by the females, but though the number of females was higher, more often no female was in the canopy during the day. Again *Ken* rarely used the canopy, although longer periods were more common for him now than in winter (Fig. 3.86c,d).

Underneath the canopy the koalas were able to use several branches with only few leaves. That part of the tree was less often used by the females than the canopy, but more often by *Ken*. The time spent on the trunk varied considerably (Fig. 3.85). *Ken* spent long periods here and, especially in summer rested here often. Prior to the Keeper's Talk the koalas climbed frequently onto these branches to await the keeper, but besides this no pattern was obvious (Fig. 3.87). In winter, the branches were used by the females more often during the night, when they did not use the canopy. In summer, this difference was not as strong.

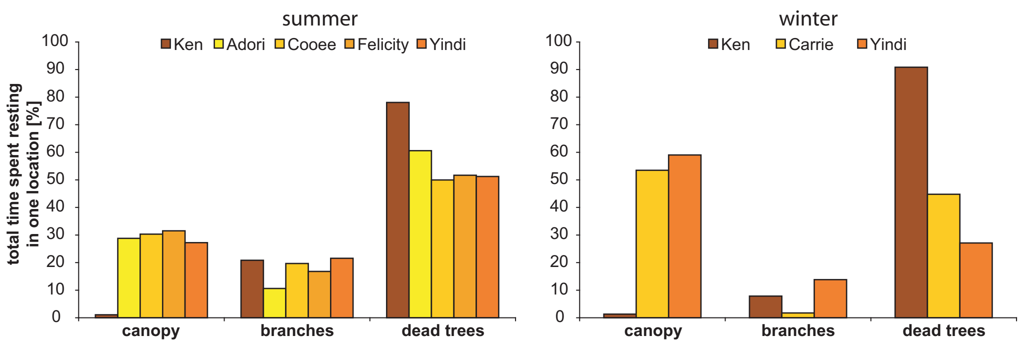

Figure 3.85: Average time spent resting in one location at Koala Walkabout during summer and winter. Percentage of time spent resting in one location during six weeks in summer and winter each.
In winter the two females spent most of their time in the canopy. *Ken* spent more than 90% of his resting time on one of the dead trees. In summer the dead trees were the preferred resting location of all koalas.

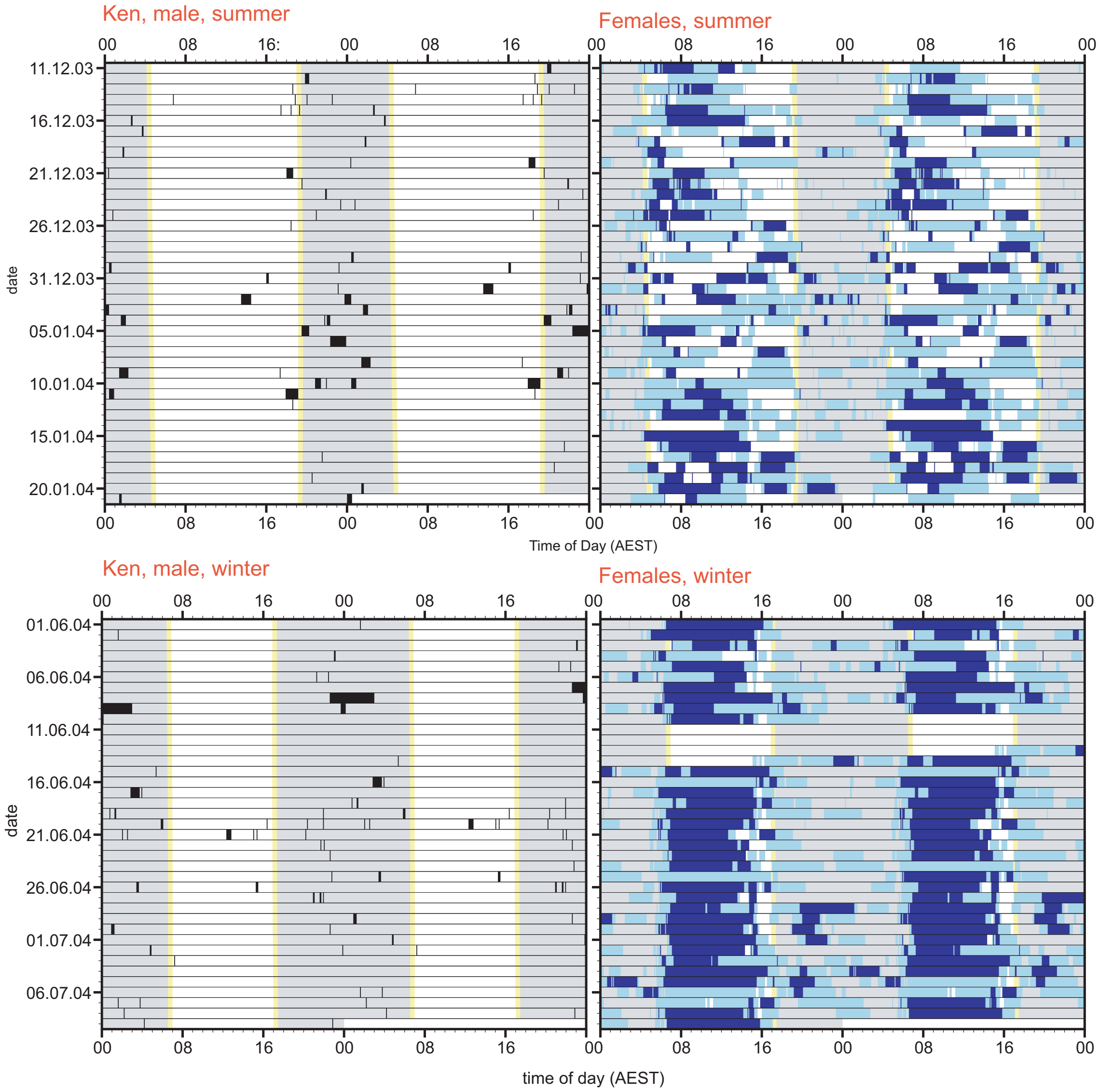

Figure 3.86: Presence in the canopy in *Ken* and the females in Southern summer and Southern winter. Double-plotted chronoethogram from 11 December 2003 to 21 January 2004 (four females) and 1 June to 9 July 2004 (two females). Black bars = *Ken* in canopy, light blue bars = one female in canopy, blue bars = two females in canopy. Background colours: grey = night; yellow = twilight.

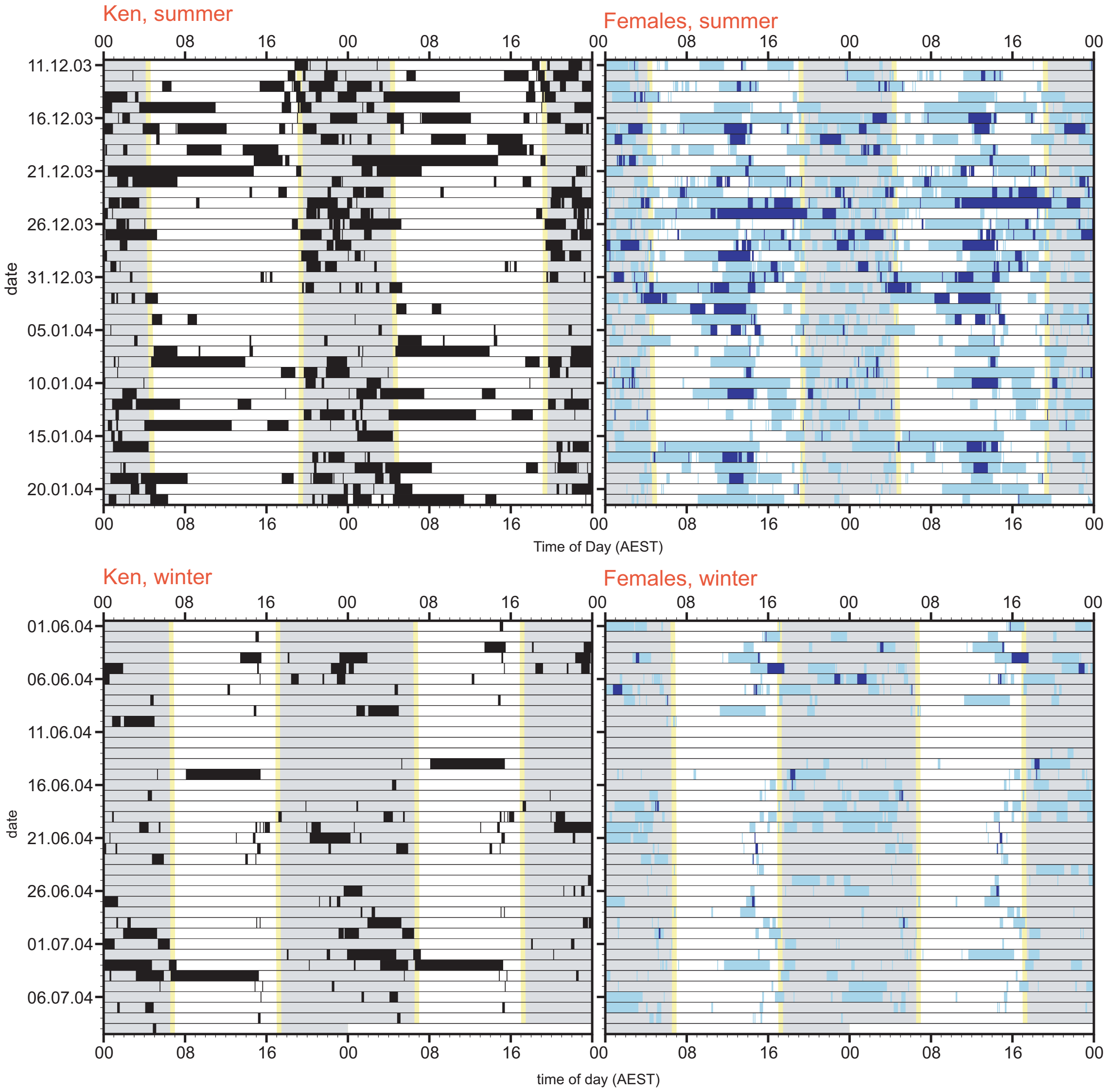

Figure 3.87: Presence in the branches underneath the canopy in *Ken* and the females in Southern summer and Southern winter.

Double-plotted chronoethograms from 11 December 2003 to 21 January 2004 (four females) and 1 June to 9 July 2004 (two females). Black bars = *Ken* in tree, light blue bars = one female in tree, blue bars = two females in tree. Background colours: grey = night, yellow = twilight.

No clear pattern was visible for the trunk, but the koalas were seen on several days in the tree prior to Keeper's Talk. *Ken* regularly stayed in the tree for longer periods of time, and had been observed there more often in summer. The tree was also used more often by the females in summer, but most often only one female is there.

3.9.2 Duisburg

In Duisburg the koalas had access to a small fig tree (*Ficus benjamini)* tree. The females had access to one tree, while the male had access to two.

Not all koalas used the fig tree. *Allora* spent more than one third of her time in the tree, especially during the day in summer (Fig. 3.88). She entered the tree in the last hours of the night, often shortly before the keepers arrived and stayed there for the morning or even the whole day (Fig. 3.89c,e). *Kambara* spent long parts of the nights and most of the morning in the tree during summer (Fig. 95 b). In winter he used the tree less often, but usually stayed there for several hours (Fig. 3.89d). The females *Kangulandai* and *Yuri* almost never used the tree, but Koomela, *Yuri*'s daughter has been observed there in several winter nights (Fig. 3.88, Fig. 3.89a). She usually used the tree during the night, while *Allora* was not there. Some squabbles have been observed between the two females, if they encountered each other in the tree.

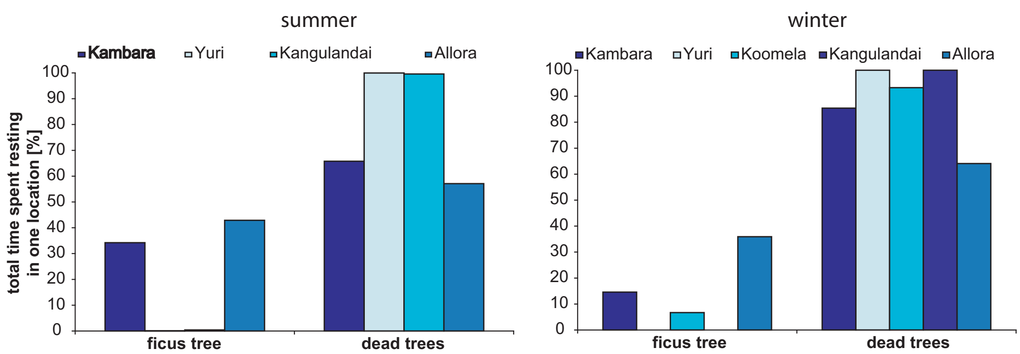

Figure 3.88: Average time spent resting in one location in Duisburg during summer and winter. Percentage of time spent resting in one location during six weeks in summer and winter each.
Most of the resting time was spent on the dead trees. The fig trees were used by *Kambara*, *Allora* and the juvenile Koomela. *Yuri* and *Kangulandai* have rarely been seen in the tree. *Allora* was using the trees most often.

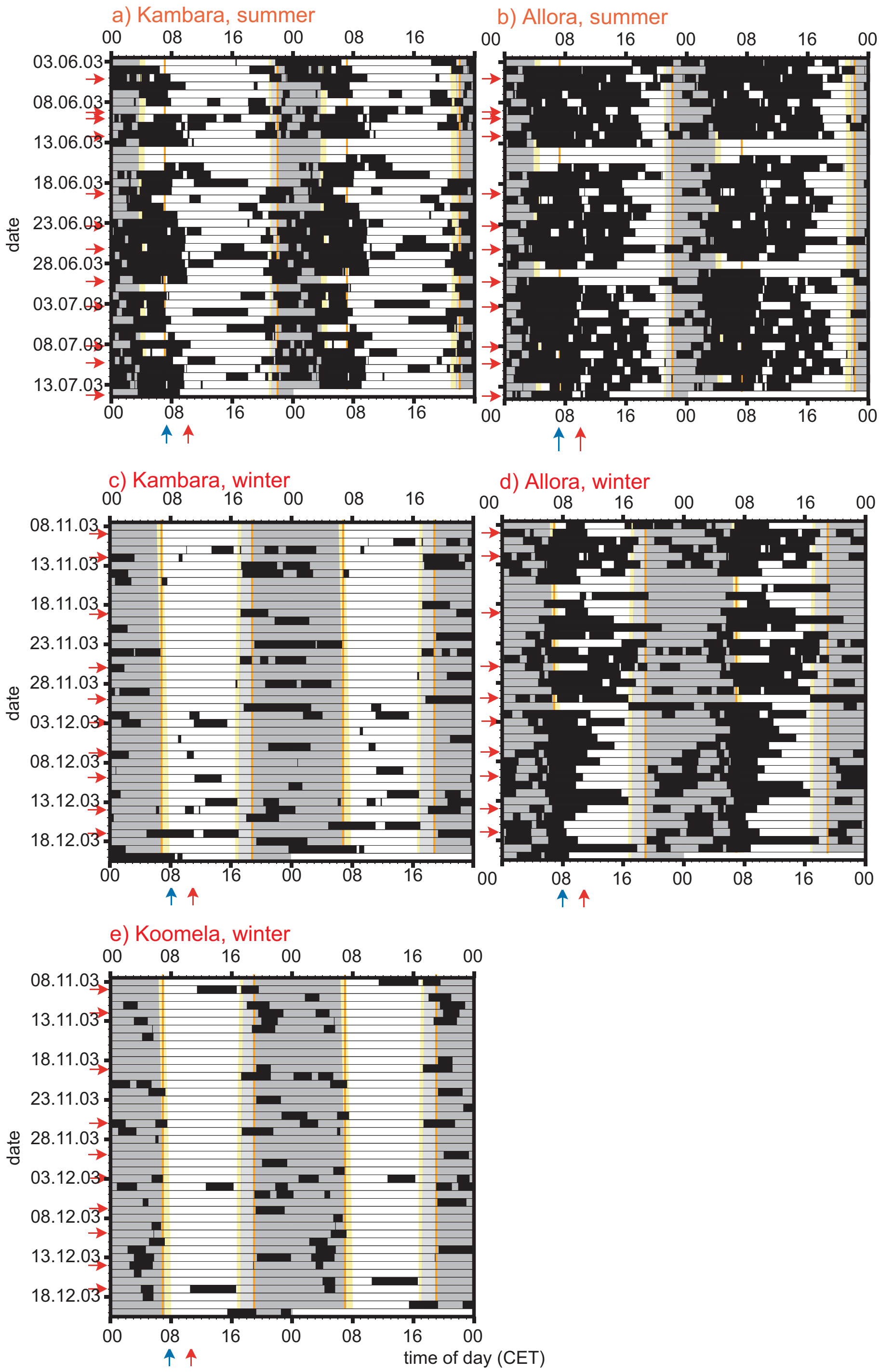

Figure 3.89: Presence in the fig tree for all Duisburg koalas in Northern summer and Northern winter. Double-plotted chronoethograms from 3 June to 14 July 2003 and 8 November to 20 December 2003. Black bars indicate presence in tree. Background colours: grey = night, yellow = twilight.
Only *Kambara*, *Allora* and the juvenile *Koomela* have been regularly observed in the tree. *Allora* spent most of the winter days and the summer mornings in the tree. *Kambara* stayed also often there in the summer mornings and nights, but less often in winter, then usually during the night. *Koomela* also stayed was in the tree mostly during the night.

We need another and a wiser ... concept of animals.
... We patronize them for their incompleteness, for
their tragic fate of having taken form so far below
ourselves. And therein we err, we greatly err. For
the animal shall not be measured by the man.
HENRY BESTON

Chapter 4

Discussion

4.1 Koala Walkabout

4.1.1 General activity pattern and acting Zeitgebers

The koalas at Koala Walkabout had the least artificial housing conditions of the study groups. Although there were seasonal variations, all koalas at Koala Walkabout showed a uniform basic pattern. There was a clear 24-hour periodicity with more activity during the night and an extended resting period in the morning. Additionally ultradian rhythms have been displayed, which were obvious during the night in all koalas, but were not displayed at daytime. The male *Ken* also displayed infradian rhythms in locomotor activity with a period length of 6.6 days. Activity peaks were also observed during dusk and dawn. In the afternoon, there was an increase in activity with a clear-cut onset of feeding at 15:30, when fresh browse was introduced by the keeper.

Individual variations between the ethograms were small. Only one female differed significantly from the others. *Yindi* is one of the two smallest koalas in the enclosure. She stayed there for almost the complete year and gave birth to a healthy joey. Like the other koalas, *Yindi* reacted to the fresh browse at the Keeper's Talk with locomotor activity, but rarely fed. Instead, her main feeding time was at dusk.

It has been shown by several authors that koalas are not strictly nocturnal, but also feed during the day. In all studies feeding was related to dusk and dawn, and there also has been feeding in the afternoon. Feeding in the morning has been rare. These activity patterns are also reflected in body temperature in unrestrained koalas (Degabriele & Dawson 1979; Nagy & Martin 1985). Temperatures were highest in the afternoon and at dusk, and lowest in the morning.

Some authors reported strong variations between individuals and days in free-range koalas (Logan & Sanson 2002a; Nagy & Martin 1985), but at Koala Walkabout daily pattern showed a strong rigidity within a certain range. Free-ranging koalas are usually studied for a short period of time and not necessarily on consecutive days. This might give the impression that activity pattern between days vary stronger than they actually do. However, free-range koalas are subject to a number of external influences like weather, changing food quality, social encounters or predators that might directly influence their activity (Kavanau & Peters 1976; Cooper & Withers 2004). In captivity, daily routine is much more monotone.

4.1.2 Entrainment and masking – competing stimuli

The activity of the koalas was clearly related to three stimuli: dusk, dawn and the Keeper's Talk (including the introduction of fresh browse). The end of feeding activity was related to dawn and sunrise. There was some relation with locomotor activity too. In *Carrie* and *Yindi* locomotor activity increased during dawn. Such pre-roosting activity is known from birds. They show high activity in the flock before they enter their roosting sites for the night (Miskimen 1960; Krantz & Gauthreaux 1975; Tomback 1978). A possible function in birds is the utilisation of the last light before night for feeding. The low light would act as an additional protection from predators (Tomback 1978). To a certain degree this might also be the case in koalas. Even so, it is possible that koalas inspect their enclosure before they decide where to rest for the next hours.

During the complete year feeding ended shortly before sunrise, usually even before dawn. In locomotor activity, the relation to sunrise showed seasonal variations. In *Yindi* and *Carrie*, there always was a distinct peak at dusk. But while in winter locomotor activity ended with sunrise, it was prolonged into the morning in summer. Such a change in phase angle difference is known from many species (Aschoff 1954). It enables an organism to adjust the necessary duration of activity to seasonal variations in day length.

The major peaks in activity were related to dusk and to the Keeper's Talk. The reaction to both stimuli differed between individuals. The strongest stimulus for feeding in all koalas but *Yindi* was the introduction of fresh browse at the Keeper's Talk. Such a reaction has also been observed at Lone Pine Sanctuary, Brisbane (Smith 1979a) and is widely known from many zoo species. At Koala Walkabout food is accessible for the koalas for almost the complete day. When food is tested as Zeitgeber in lab experiments, it usually only influences the activity if food access is restricted to a short period of time (Aschoff 1958). Therefore, such a strong reaction of the koalas would not be expected. However, quality of the browse is not constant during the day. Koalas are very particular in the choice of single leaves. Water content is important, since the koalas satisfy their complete water demand by leaf consumption (Lee & Martin 1988). In the course of the day the leaves lose water, so fresh leaves are more preferable. A number of other parameters, including content of lignin and several toxins influence the choice of the koala (Lee & Martin 1988; Hume & Esson 1993). In a group of koalas, food competition might be important in ensuring an adequate intake of nutrients and avoiding high intakes of toxins.

In some of the koalas, particularly *Ken* and *Yindi*, a second band of feeding was visible at dusk. Robbins and Russell (1978) report feeding related to dusk in free-range koalas. It seems that dusk is a natural feeding time for koalas (for overview see Cronin 1987; Lee & Martin 1988). However, *Carrie* did not show a feeding band at dusk, and in *Ken* and *Adori*, feeding at dusk was not observed at all times of the year. Instead, these three koalas showed a strong band at the Keeper's Talk. It is questionable whether the Keeper's Talk really is a Zeitgeber or simply a masking factor directly triggering food intake.

One characteristic of Zeitgebers is anticipatory activity. Indeed there was an increase in locomotor activity up to 75 minutes prior to the Keeper's Talk. However, there seemed to be another reason for the activity. The post-/pre-stimulus-time-histogram (PSTH) shows that locomotor activity increased right after the removal of the old browse. Additionally, there were some external signals shortly before the Keeper's Talk started. Usually a group of visitors was waiting in front of the enclosure after 15:15 and the koalas were able to see the keeper approaching with fresh browse up to ten minutes before he actually entered the enclosure. So it appears more likely that the Keeper's Talk masked the endogenous periodicity.

However, there is a hint to a slight effect of the Keeper's Talk/fresh browse as a Zeitgeber: When the Keeper's Talk was delayed by one hour on 28 March 2004, *Ken* and *Adori* showed increased locomotor activity, but not *Carrie* and *Yindi* (see Fig. 65-68). When food presentation was delayed by three hours on 31 January 2003, *Ken*, as well as *Cooee* and *Felicity*, again showed increased locomotor activity, but not *Adori* and *Yindi* (see Fig. 72). This increased activity might be a transient and suggests that some of the koalas reacted to the delayed food. Even so, masking does not necessarily trigger an immediate response. In this case the koalas might react, because the first in a series of external signals, the removal of the old browse, took place but was not followed by the next signal. This deviation from daily routine might have triggered restlessness.

An advance of one hour in food presentation on 31 October 2004 resulted in locomotor activity in all koalas after the old browse had been removed, and in some minutes of locomotor activity before the koalas finally started to feed. It is possible that the advance was not expected by the koalas and therefore triggered higher locomotor activity. This can be the cause by a Zeitgeber, but also by a masking factor, which might influence the rhythm via direct induction of activity (Aschoff 1981b).

During the year, there are clear changes in priority of food introduction and dusk. While Keeper's Talk and dusk act independent from each other in summer, this changes in autumn. As days got shorter and additionally the Keeper's Talk was delayed by one hour due to the change back to Australian Standard Time, both stimuli moved closer together. Feeding began with the Keeper's Talk, lasted for most of the afternoon and was not resumed during dusk. In March and April as well as in September and October, there were transients in feeding in *Ken* between the Keeper's Talk and dusk. It seems that during this time the Zeitgeber dusk lost its strength. Instead the food presentation caught the freerunning rhythm and became the major signal for the daily periodicity. Finally food presentation was so strong that there was no feeding related to dusk in winter.

In *Yindi*, there was competition between dusk and the Keeper's Talk too, but with a different outcome. In summer *Yindi* also had two feeding bands. When dusk advanced towards the Keeper's Talk, the latter one lost its strength until finally feeding was primarily observed at dusk. In opposite to *Ken*, the natural Zeitgeber overrode the potential masking factor. In spring, dusk as Zeitgeber became stronger again and transients reappeared. Finally both stimuli acted independently from each other and again there were two separate bands.

This change in Zeitgeber strength has been described by Aschoff (1954). He also states that Zeitgeber strength is not absolute, but differs between individuals. The ethograms from Koala Walkabout show such individual differences. *Yindi* was the only koala in which dusk was stronger than food presentation. In *Ken* there was a clear competition between both stimuli, until finally food took over. *Adori* shows sign of competitive entrainment too, but not as strong as *Ken*. *Carrie* however did not show any entrainment to dusk, but only reacts to the Keeper's Talk. Nevertheless locomotor activity and the end of feeding in *Carrie* were clearly related to sunrise.

4.1.3 Time budget - comparison to free-range studies and seasonal variations

Between 18 and 19.5 hours (75 - 79% of the day) of the day were spent resting. Although the koalas were not strictly nocturnal, resting was more common during the day, while feeding and especially locomotion were more often displayed at nighttime. Free-ranging koalas rest for 18 to 22 h (75 – 92% of day) depending on age and physiological state of the koala. Like their captive counterparts, they are not strictly nocturnal. Thus, resting times of the koalas at Koala Walkabout did not differ from free-ranging individuals. However, resting times of 19 hours have only been reported from lactating females and males with high tooth-wear (Logan & Sanson 2002a, 2003). The latter should not be the case at Koala Walkabout. Also, high locomotor activity is partly the case for increased activity in such koalas, since they need more time to forage for food, which is not the problem at Koala Walkabout. The major problem might be the length of observation intervals. In 9.2% of intervals, locomotor activity was shorter than five minutes but counted as such. This would add more than one hour to the average resting time.

It is generally difficult to compare locomotor activity at a zoo with field data. Aside from the lengths of observation intervals, there was neither the possibility for long-distance movements nor the necessity to move between trees for food. The koalas needed to come to the ground only to reach two of the four dead trees. This usually took place at night, though the male regularly changed trees during the day, especially during the Keeper's Talk. Explorative behaviour on the ground was rare and almost exclusively seen in the male. However, when new logs had been brought into the enclosure, once the male came to the ground to explore them.

Locomotor activity is often triggered by another koala, which passed nearby or actually drove the first koala away. *Ken*, the male, surprisingly was the koala that moved away most often, though he was about twice the females' size. However, it has been reported before that females are more aggressive than males. They rarely initiate a fight, but use vocal warnings and do not draw back (Cronin 1987). Open aggression or even contact has rarely been observed at these occasions, but vocal interactions cannot be excluded, since they have been frequently observed during direct observation. *Yindi*, the smallest female, was the koala in which avoidance behaviour was observed second most often and *Ken* drew back less often from her than from the other two females, so size might play a role too.

Feeding was the major activity, accounting for 2 – 3 hours per day and was displayed in bouts of up to two hours. *Ken* fed significantly longer than the females, basically because single feeding bouts were longer. The higher amount of feeding can be explained by his higher body mass; *Ken* weighed between 11 and 13 kg during the study, while the females' weights did not exceed 7 kg. Males get generally more branches than females at Taronga Zoo.

In free-ranging koala considerable differences in the time spent feeding between individuals and studies have been found, ranging from one to five hours . The total amount of time spent feeding seems to depend on food quality, lactation and tooth wear (Logan & Sanson 2002b, 2003). Food quality at Taronga Zoo was generally good, though not free from seasonal variations (see below) and it can be assumed that captive koalas should not suffer from food shortages. Therefore it is not surprising that the koalas at Koala Walkabout are in the medium range of feeding time.

An average feeding bout at Koala Walkabout lasted 31.1 minutes, but generally there is a great variation between single bouts. Smith (1979a) found an average length per bout of 19 minutes at Lone Pine Sanctuary. This is considerably shorter than at Koala Walkabout, but he observed only during the day, when shorter bouts were more common at Koala Walkabout too. Also, mean values seem to be an inadequate measure for bout length, for long bouts are rare and bouts of only few minutes have been observed more frequently. Robbins and Russell (1978) report that bouts lasted between 5 and 125 minutes in the field. Fifty-two percent of the bouts had a duration of 30 minutes or less. This is similar to Koala Walkabout. At Lone Pine Sanctuary, feeding bouts lasted up to 90 minutes, but most of them were shorter than 20 minutes (Smith 1979a), which again was shorter than at Koala Walkabout. Interruptions of feeding bouts were frequent at Koala Walkabout, especially in the afternoon, when more than one koala fed at the same time, but the koalas usually resumed feeding immediately. With 20 to 30 koalas per enclosure (102 m^2), group size at Lone Pine has been considerably bigger than at Koala Walkabout, so interruptions might have been more frequent. Such encounters are very rare in the wild, but there, short interruptions in feeding have been reported too (Robbins & Russell 1978).

There were significant seasonal variations in time budget, which were most obvious in feeding. In summer, the koalas spent a comparatively lower amount of time feeding than in the rest of the year. Feeding increased towards winter, in *Ken* reaching a maximum in May and June. From August on the levels decreased again towards summer. Mean values of the females were lower than in *Ken*, but they reached their maximum level in April and remained high for the rest of the study.

The browse at Taronga Zoo is obtained from eucalyptus trees from the surrounding areas. Therefore food quality changes through the year. It is not known if the observed koalas ate a higher amount of food, but in winter they might need more time to find the right leaves on the branches. Also the koalas had a competitor for the food, which might lessen food quality too. Between April and September ringtail possums (*Pseudocheirus peregrinus*) and brushtail possums (*Trichosurus vulpecula*) visited the enclosure at night and fed on the eucalypt leaves. At this time of year their other food sources were low and the browse at Koala Walkabout would be an additional supply (Benesch & Hill, *unpublished* *data*).

While in *Ken* total feeding time decreased towards summer, values remained high in the females. Two of the three females, *Yindi* and *Carrie* had pouch young born in March respectively May. Energy requirements are higher in lactating females (Krockenberger 2003) and food intake increases up to 36% (Krockenberger 2003). Logan and Sanson (2003) found increased values for feeding in free-ranging lactating females. They also found increased values for locomotion, which is not the case at Koala Walkabout. This might be explained by the fact that the zoo koalas do not have to forage and change trees for their food, but get an adequate amount of fresh browse from the keeper. Therefore it is not necessary to expend more energy for foraging.

In *Ken* higher amounts in locomotor activity have been observed in summer. Locomotor activity was high in all koalas in January. During this month four copulations and several mating attempts took place. In the second summer *Ken* was observed frequently to approach females and check their readiness for mating, but the females did not show any interest, still having dependent pouch young.

Resting time was highest in February. At this time, four females have been in the enclosure, the highest number of koalas during this study. It could be expected that this would increase activity, but it obviously did not.

Feeding and locomotor activity were more often observed during the night, while resting was slightly more common during the day. In feeding the day:night ratio changed during the year: In winter and spring feeding was particularly increased during the night. In the females this effect was increased by a change in group composition. During March and July, only *Carrie* and *Yindi* were in the enclosure. *Yindi* generally had a highly negative day:night ratio, while *Adori*, who had been removed for that period, showed the comparatively highest amount of feeding during daytime. These two extremes might have levelled out each other in the other months. However, in *Carrie* feeding at night becomes more common during the winter months too. So season itself had some influence on the females.

Locomotor activity differed between months too, but there was no seasonal pattern. Day:night ratio differed strongly between single days, so there might be a number of external influences which could not be identified. Resting was only slightly more common during the day. This did not change much during the year, but in winter there was more resting during daytime, probably to the higher amount of feeding at night.

Conclusion: Koalas at Koala Walkabout, Taronga Zoo, displayed clear circadian rhythms in feeding and locomotor activity. Koalas were not strictly, but mainly nocturnal. Activity patterns *and time budget varied little between individuals and days and were comparable to free-ranging koalas. Light acted as zeitgeber, but the keeper, especially the introduction of fresh browse had a strong influence on the activity patterns. However, it is not clear, if food introduction acted as zeitgeber or masking. Zeitgeber strength and time spent feeding showed seasonal variations as expected in koalas. Based on this analysis, the koalas at Koala Walkabout can be used as reference group for the behaviour of zoo koalas.*

4.2 Comparison of zoos

4.2.1 Activity patterns

To compare the three zoos, six weeks in winter and summer each have been analysed. There have been clear differences in the behavioural patterns of the three zoos. Koala Walkabout in Sydney was the only zoo where the ethograms of the individual koalas were uniform. Characteristic for the circadian patterns was the discrimination between day and night, with frequent activity at night time and resting during the morning. Also, in all koalas was a clear reaction to fresh browse at the Keeper's Talk, though there were small individual differences.

The Duisburg koalas, on the other hand, showed distinct individual differences. Only two of the females, *Yuri* and *Allora* discriminated between day and night. The female *Kangulandai* showed no day-night discrimination, while the male *Kambara*, especially in winter showed a tendency to diurnality. Also, the reaction to the keeper differed between the individuals. *Kambara* and to a certain degree *Kangulandai* clearly reacted to the keeper. The other two females, which rested most of the day, did show little reaction to the keeper's activity.

The two koalas at Vienna Zoo also showed no correspondence in their behaviour. The male *Bilyarra* had a distinct day-night pattern, while in the female *Mirra Li* no obvious pattern was detectable.

In all koalas activity was generally higher during the night than during daytime. However, daytime pattern differed significantly. While the koalas at Koala Walkabout rested in the morning, the koalas in Duisburg and Vienna showed activity peaks related to the keeper. In some cases there was no activity prior to the keeper's appearance. Instead, especially in Vienna, the koalas were asleep. The keeper's presence did not trigger activity at Koala Walkabout in the morning, but in the afternoon, when browse was exchanged. Independent from the keeper, koalas at Duisburg and Vienna displayed some activity in the afternoon too. The influence of the keeper on activity will be discussed later.

4.2.2 Time Budget

In all three zoos, most of the time was spent resting. The koalas at Koala Walkabout rested for the lowest amount of time, between 18 and 19 hours. *Mirra Li* at Vienna Zoo rested for the longest time, 19.5 hours, but did not differ significantly from the Duisburg koalas. All koalas were well within the resting times of 18 to 20 hours reported for free-ranging koalas (Sharpe 1980, Nagy & Martin 1985, Mitchell 1990, Logan & Sanson 2002b, 2003).

The small differences in time budget are interesting if compared to the ethograms. *Mirra Li* rested for a high total time in winter, but her ethogram shows many short activity bouts at very high frequency. *Kambara* and *Kangulandai* in Duisburg also had a high frequency of short activity bouts, though not as intense as in *Mirra Li*. *Kambara* had the highest resting time of the males, but *Kangulandai* had the significantly lowest resting times of the Duisburg females. Wood (1978) states that frequent interruptions of resting time might be a stressor for koalas. In the case of *Mirra Li*, *Kangulandai* and *Kambara*, resting is not interrupted by external stimuli, so the high frequency of behavioural changes in these koalas might be a sign for unsettlement or distress. However, none of these koalas has been diagnosed with weight or health problems. The long total resting times might reflect sleep quality: short resting bouts are less effective than long once and it is thinkable that *Mirra Li* and *Kambara* needed to compensate this by a higher total amount of resting.

Feeding was the major activity in all koalas. Even so, feeding times differed severely between zoos. No relation to feeding schedule was detectable: with 3.5 to 4.75 hours per day, the koalas in Duisburg fed for a considerably longer time than those at the other two zoos with 2.5 to 3.25 hours. None of these times differed from the one to five hours reported in free-range koalas .

Feeding pattern differed significantly between individuals. Increased feeding around sunset or during dusk as reported in free-ranging koalas has only been observed in *Yindi* (Sydney), *Kambara*, *Yuri*, *Kangulandai* (Duisburg) and *Bilyarra* (Vienna). However, increased feeding levels in the afternoon have been observed frequently in the other koalas. Nagy and Martin (Smith 1979a) found a feeding peak between 08:00 and 10:00, which is not found at Koalas Walkabout, but in both koalas in Vienna. In Duisburg, *Kambara* and *Kangulandai* showed feeding peaks later in the morning. However, activity in the morning might be related to keeper's activity (see below).

There were also considerable differences regarding feeding bouts. As said before, the lengths of single feeding bouts varied greatly at Koala Walkabout. A histogram for six weeks in winter and summer each shows durations from 5 to 120 minutes. The average length of a bout was 26.5 minutes. However, this value does not reflect the feeding pattern sufficiently, for short bouts are considerably more common than long bouts. The histogram for Duisburg Zoo is fairly similar to Koala Walkabout, though it peaks at slightly longer bouts. Therefore the average length of 34.6 minutes was considerable longer. However, the daily number of bouts was similar in both zoos. At Vienna Zoo, feeding bouts were considerably shorter. This is already obvious in the ethogram but gets even clearer in the histogram. Bouts did not last longer than 75 minutes and most bouts were even shorter than 30 minutes, with an average of 18.6 minutes. However, there were significantly more feeding bouts per day than in the other zoos, so the total amount of feeding time did not differ from the other koalas.

The reason for this is difficult to find. Short feeding bouts have also been found at Lone Pine Sanctuary, where 20 to 30 koalas had been kept on 100 m^2 (2002a; 2003), roughly the size of Koala Walkabout (113 m^2). It is likely that the koalas at Lone Pine interrupted each other frequently, resulting in short feeding bouts. But this cannot be the case in Vienna, where the koalas are separated from each other. Feeding bouts in free-ranging koalas vary considerably. Logan and Sanson (Kindemi *pers. comm.*) found that the average length of feeding bouts lengthens with tooth-wear (as does total time per day feeding) and are particularly long in lactating females. In winter, all observed females in Sydney and Duisburg were lactating, in summer this was the case in all Duisburg females and most of the Sydney females. This might also be the reason for the high total feeding time per day, for lactating females have higher energy requirements (Krockenberger 2003). However, the males in those zoos have long feeding bouts too. Given that prolonged feeding times are lacking in the Vienna female too, it must be considered a possible symptom of unsettlement or stress.

It is not clear why the koalas in Duisburg fed for a considerably longer time than the others. None of the koalas was overweighed, although *Kangulandai* had visible fat deposits on the upper arm. Also, the Duisburg koalas did not feed an abnormal high amount of leaves .

In winter feeding times were significantly longer than in summer in all koalas but *Kambara* and *Allora*, in which they did not differ. As discussed for Koala Walkabout, food quality is lower in winter, resulting in a longer amount of time to find appropriate leaves. Additionally all joeys were bigger in winter than in summer, so we can assume that in winter the females had higher energy requirements.

As discussed above, locomotor activity from this study is difficult to compare to free-ranging studies. But there were clear differences between the three zoos. With 113 m^2, Koala Walkabout was the biggest enclosure; enclosures in Duisburg and Vienna measured only 22 m^2. Also, trees at Koala Walkabout were up to 2.5 times as high. Therefore, the koalas there had the biggest space available for movements. The distances between possible resting places and food vases were bigger. Hence, it is not surprising that in winter locomotor activity was highest there, since feeding was increased too. However, in summer locomotion is highest in Vienna, particularly in the male. This is rather surprising, for the koalas in Vienna rest next to or in their food. At Koala Walkabout the koalas sometimes changed the tree during a feeding bout, but in Vienna, the koalas very frequently moved between the vases. Since they are not disturbed by other koalas, this might be a sign for unsettlement.

In Duisburg locomotor activity was generally low. The koalas often sat close to each other, avoidance behaviour as observed at Koala Walkabout was rare. Also the keepers did not trigger activity as in Vienna. The koalas came rarely to the ground, even at night, and intensive locomotion (Loc3) was rare.

In most cases the koalas would move directly from one place to another and settle down (Loc2). Such simple relocations were equally common in Sydney and Vienna, but the differences between places were usually bigger at Koala Walkabout. Places were often changed for food intake, but at Koala Walkabout koalas also avoided each other. This was rare in Duisburg, where *Yuri* and *Kangulandai* sat next to each other regularly.

Sometimes koalas simply moved to a fork somewhat higher and lower (Loc1). This was most common in Vienna. Intensive locomotion (Loc3) was often performed on the ground, but at Koala Walkabout the females regularly jumped between trees on higher levels. This was particularly common during dawn. Jumping had not been observed at Duisburg or Vienna Zoo. At Koala Walkabout the male and some of the females came to the ground for exploration, as did the koalas in Vienna. Koalas in Duisburg rarely came to the ground and then usually only briefly. While the koalas at Koala Walkabout needed to come to the ground to reach certain trees, this was not the case in Duisburg and Vienna. However, *Mirra Li* drank frequently and both Vienna koalas climbed into the plant tubs regularly. This might be a substitution for the missing trees. Even so, the high levels of locomotor activity and the comparatively frequent change of position might also be a sign of unsettlement.

Conclusion: Although time budget did not differ dramatically between zoos, activity patterns clearly did. While the koalas at Koala Walkabout were very similar in their circadian patterns, the koalas in Duisburg and Vienna displayed distinct individual differences. Also not all koalas in Duisburg and Vienna displayed a day-night pattern. Unstructured activity patterns were in some koalas combined with high total resting times, probably because short resting periods were *of low quality. Feeding bouts in Vienna were generally shorter than in the other zoos. Locomotor activity was high in the biggest enclosure (Sydney), but also in Vienna. High locomotor activity, unstructured activity patterns and short resting bouts are a sign for unsettlement or stress.*

4.3 Zeitgeber and masking in indoor enclosures

In Vienna and Duisburg light regime was more complicated than in Sydney, for koalas experienced the natural light through large skylights and artificial lighting with constant day length. Natural variations in day length were much stronger in Vienna and Duisburg than in Sydney. To compensate the shorter winter days, light time was artificially extended. Generally, only two females in Duisburg and the male in Vienna discriminated between day and night. Their patterns were similar to those at Koala Walkabout. In the other three koalas, activity was more evenly distributed through the 24 hours.

Light showed Zeitgeber properties in all koalas, but its strength differed between individuals and seasons. In summer there was a close relation between sunrise and the end of activity in all koalas. No relation to the beginning of the artificial day was seen. In the afternoon there usually were several activity bouts. All koalas but *Mirra Li* displayed a peak in activity around natural dusk. During this time the lights were switched off too, so both stimuli merged. This pattern was basically similar to that observed at Koala Walkabout.

In winter, the relation to twilight became more complex. In Vienna activity was slightly reduced when the lights were switched on, but the peak at natural dawn is more likely keeper related. In Duisburg activity peaked in the two dark hours before the lights were switched on and was reduced after that, but *Kambara* and *Kangulandai* had a small peak during natural dawn. However, this might be keeper related too. In the evening natural dusk had no impact in Vienna, but there was an activity peak after the lights had been turned off. The koalas at Duisburg Zoo had two peaks, one at natural dawn and one when the lights were switched off.

It seems that while most koalas were entrained to natural light in summer, the artificial light regime was stronger in winter. The artificial light probably had a higher intensity than winter sunlight, especially during the afternoon. However, at least in Duisburg there was some relation to natural dusk. In summer natural dawn was well before the lights were switched on, which did not result in a similar change of light intensity as natural dawn. Thus the koalas did not react to the second stimulus.

It appears as if the artificial light regime does not entrain the koalas adequately, especially in winter. *Kangulandai*, *Kambara* and *Mirra Li* did not show a distinct day-night pattern. Relation to light was generally low, but these koalas reacted strongly to the keeper. In summer the only light related regularity was a band of resting in the morning, but this was not observed in winter. Also, the difference in activity between day and night was clearer in summer than in winter. *Mirra Li* and *Kambara* were even slightly diurnal in winter. Additionally *Bilyarra* reacted more immediate to lights on/off in winter, while in summer there were distinct phase angle differences between sunset/sunrise and onset/end of activity. However, these phase angle differences might be due to natural seasonal variations. Most koalas had a 24 hour periodicity in their behaviour, but not *Mirra Li* in winter. Instead, feeding bouts appeared with a significant period length of 3.43 hours, which might be an endogenous rhythm of the digestive system, while the complete organism is not entrained to light.

The seasonal differences suggest that the artificial light regimes were not optimal for the studied koalas. In winter, day length in Australia is about 10 hours, 1.5 hours longer than in Central Europe. To compensate this difference, artificial light is used. However, with the combination of natural and artificial light, the koalas experience four "twilights" per day, two natural and two artificial with up to two hours difference between each other. Instead of the natural lights dusk and dawn stimuli, the pacemaker gets the signal lights on – lights on – lights off – lights off. In Duisburg this results in four activity peaks related to light. In summer artificial and natural light regime are closer together, therefore the stimuli might merge with each other and only two activity peaks are displayed.

Since koalas are nocturnal, most of their natural feeding time is at night, though they also feed in daylight (Kindemi *pers. comm.*). Therefore the longer winter nights in Europe might not be a problem for captive koalas. If so, there would be no need to extend day length. On the contrary the observations show that in summer activity is prolonged into daytime. Maximum day length in Australia ranges from 13 in the North to 14 hours in the South; maximum day length in Vienna is 16 hours, in Duisburg 17 hours. If day length is to be adjusted to Australian conditions, it would be more useful to shorten day length in summer.

Conclusion: In all zoos light showed Zeitgeber properties, but Zeitgeber strengths changed with season. In summer, entrainment to day/night was obvious, and activity peaks were related to natural light. Artificial lighting seemed not to be sufficient to entrain the koalas, for discrimination between day and night were weaker and koalas showed activity peaks related to natural and artificial light. It is also questionable whether it is necessary to artificially extend the day in winter.

The difference in day length in summer is bigger between Europe and Australia than the difference in day lengths in winter. Since koalas are nocturnal, an extension of summer nights might be more useful than an extension of winter days.

4.4 Influence of keeper and handling

Intensity of handling severely differed between Koala Walkabout and the two European zoos. Most of the koalas at Koala Walkabout have not been trained for extensive handling. Koalas were usually grabbed by their wrists from behind, for koalas often resisted by moving away, snarling or even scratching. At Vienna and Duisburg Zoo koalas have been handled at least once a week from early age. The Vienna keeper carried the koalas on their arms like a toddler and the koalas stay there for several minutes without resistance. At Duisburg Zoo koalas are usually handled similar to Taronga Zoo, but resistance is rare in the females and the young koalas are sometimes carried on the keeper's arm. It is generally discussed, if regular handling is a stressor for a zoo animal or if the training familiarises it with the keeper and actually reduces stress in the long-term. The ethograms show different reactions on the keeper, which will be discussed in detail now.

4.4.1 Cleaning

At Taronga Zoo the koalas did not react during the brief morning cleaning. There was little contact to the keeper and often the koalas sat high up in the trees. The only exceptions were *Yindi* and *Lowanna*. Both females had been trained for intensive handling by education officers. Occasionally they actively approached a familiar keeper and tried to climb on her arm, which usually was allowed by the keeper for a few minutes. For these two koalas the keeper probably was enrichment in daily routine, while the other koalas were not disturbed in their rest.

In the afternoon old browse was removed and for about an hour the koalas were not able to feed. In some cases the koalas moved away when the keeper took away the branches they were sitting in, but this interruption was brief. Sometimes koalas fed when the browse was removed. Often the keeper would leave some branches for the feeding koala, but in the case that all food was removed, the koala would rest until Keeper's Talk. Generally the disturbance by the keeper was brief.

In Duisburg the keeper entered the enclosure several times during the morning. As in Sydney the females did not interrupt their rest, but sometimes changed their roosting place, when the browse they were sitting in was removed. They accepted brief contact with the keeper. *Kambara* showed some activity at this time, but on most days he was resting too. Activity might be triggered by two other stimuli than the keeper. First, he was able to see the second male through the open door and frequently bellowed. Second, on some days he tried to leave the enclosure, possibly to enter the females' enclosure as has happened before. This is a social enrichment for the male.

The two koalas in Vienna reacted much stronger to the keeper. Locomotor activity in *Mirra Li* increased before the keeper entered the enclosure, probably because *Mirra Li* was able to hear her. Since the keeper always entered at a different time, the koala cannot be entrained to her coming. *Bilyarra* became more active around the keeper too, but not as much as *Mirra Li*. The female actively approached the keeper and was regularly picked up and carried around. Particularly for her the morning cleaning is enrichment.

Generally none of the koalas seem to be stressed by the keeper in the morning. If direct contact was initiated by the keeper, the koalas did resist. Some koalas actively approached the keeper. Therefore the interaction between keeper and koalas can be considered as enrichment or at least as unproblematic disturbance.

4.4.2 Food presentation

In both European zoos fresh browse was introduced in the morning. The koalas in Duisburg did not react on the removal of the browse. When on average 45 minutes later fresh browse was brought in, only *Kambara* and *Kangulandai* began to feed immediately. *Allora* and *Yuri* mostly stayed inactive and started feeding in the afternoon or evening.

In Vienna, old browse was directly exchanged against fresh browse. *Bilyarra* started to feed immediately on most days, but *Mirra Li* only did this in winter. In summer she fed later in the morning. A second introduction of fresh browse in Vienna was at 10:20, right after the weighing. At this time, both koalas usually rested. *Bilyarra* often resumed resting and ignored the fresh browse, but in *Mirra Li* this was the main feeding time, but her reaction was not as strong as that of the koalas at Koala Walkabout. There, locomotor activity was increased after the old browse had been removed and ended when fresh browse was introduced. Most koalas then started to feed immediately. The feeding bout at the Keeper's Talk was one of the longest in the day.

The different feeding times triggered different responses from the koalas. The koalas in Sydney had the highest feeding peak of all and they were the only koalas that were frequently active prior to the food presentation. As discussed above, the Keeper's Talk even overrode the Zeitgeber dusk in some koalas. In Duisburg, mostly the koalas did not react on the fresh browse even if the browse was right in front of them, but fed later in the afternoon and at night. This is the feeding time known from free-ranging koalas

Anticipatory behaviour is missing in both European zoos too. Even the removal of the old browse in Duisburg does not trigger locomotor activity which could be seen as expectation resulting from a direct action of the keeper. So, feeding in the morning does not appear to be a strong stimulus. The afternoon might be a better time for food presentation, particularly if it is used to trigger activity for the visitors.

4.4.3 Weighing

Weighing is widely accepted as tool to monitor health state in koalas. The Australian Exhibited Animals Protection Act (2001) requires monthly weighing for captive koalas, San Diego Zoo (1978) recommends daily weighing if possible. However, Wood (Degabriele & Dawson 1979) warns that weighing itself, especially if it interrupts resting and feeding times, might cause stress in koalas.

Koalas at Koala Walkabout were weighed monthly during breeding season and less often in the remaining year. In the females the pouch was usually checked for joeys too. At the beginning of the catching, the koalas usually rested and did not start to move around while the keepers prepared their equipment. Usually a koala started to climb out of reach when the keepers tried to catch it. It took up to ten minutes to catch a koala, sometimes longer. During the pouch check the koalas tried to break free and frequently snarled and tried to scratch or bite the keepers. After the release *Ken* settled down within the next five minutes. The females moved around longer, but often stayed close to the keeper to watch. Some locomotor activity was observed in the following 90 minutes, but the remaining day did not differ from the other days.

The koalas in Duisburg were weighed twice a week at 11:00. Some of the koalas, mostly *Kambara* and *Kangulandai*, were feeding at this time. Usually the keeper just took the koalas at their wrists, carried them to the scale and back. Feeding usually ceased during the preparation and there was some locomotor activity afterwards in the females, but all koalas settled down quickly. *Yuri* and *Allora* mostly resumed resting immediately.

At Vienna Zoo koalas were weighed daily at 10:15. The ethogram shows that there was very little activity prior to the weighing. Often the koalas were actually asleep when the keeper picked them up. After the weighing they were carried around for a minute on the keeper's arm and than returned to a fork. *Mirra Li* regularly stayed awake afterwards and started to feed when fresh browse was introduced several minutes later. *Bilyarra* usually went back to rest and did not react on the fresh browse.

Generally the catching and weighing at Koala Walkabout had the highest impact on the koalas and it can be assumed that the koalas were under stress. But none of the koala panicked and they settled down quickly. Also, the catching took place very rarely. Therefore, the long-term consequences for the koalas are probably very low. At Duisburg Zoo and Vienna Zoo the koalas were used to daily handling and did not resist the keeper. In Duisburg, koalas often fed before 11:00, but particularly *Yuri* usually rested. After weighing, they resumed whatever they had done prior to handling. Activity pattern did not differ between days with weighing and days without. In Vienna however, the koalas were regularly interrupted in a resting period. The female stayed awake afterwards, but not the male. Most koalas in this study had extended resting periods in the morning and body temperature of unrestrained koalas were low around 10:00 (Nagy & Martin 1985), so the interruptions would take place in the physiological resting time of the koalas. Although animals seem to be calmer at these times, the physiological stress reactions are considerably higher than during the physiological time for activity (Gatternmann & Weinandy 1999). Frequent interruptions of resting periods are stressful to koalas and have to be avoided (Wood 1978). Therefore, weighing should not take place in the morning, but in the afternoon or evening.

4.4.4 Change of weighing time at Vienna Zoo

Based on this hypothesis, weighing time at Vienna Zoo has been shifted to 16:00 in the afternoon. At this time, regular feeding periods have been observed in both koalas. In the two weeks prior to the change, the ethogram clearly shows that *Bilyarra* is interrupted in his rest by the weighing and has no interest in the fresh browse but resumes resting immediately. On the first day of the shift, *Bilyarra* rests uninterrupted for seven hours before he starts feeding from his own volition. After he is weighed, he immediately starts feeding on the fresh browse. For the remaining four weeks of observation the pattern stays similar. This shows that *Bilyarra* is much more receptive for food in the afternoon and is probably less disturbed by the handling.

In the female the change was not as effective. There was little structure in the ethogram during the first two weeks. Generally, locomotor activity was high at this time. On most days the weighing was followed by some locomotion and a short feeding bout. In contrast to the male there is still activity at 10:30, though there is a regular feeding band at 16:00. After two weeks, the 10:30 peak in the ethogram disappears, but there still is no regular resting in the morning. It seems that *Mirra Li* lacks an endogenous stimulus for extended resting in the morning. However, activity bouts are generally less frequent in the morning.

It might take longer than the four weeks of observation to manifest a change in activity pattern.

If weighing had acted as a Zeitgeber, the shift would be followed by transients, not by an immediate change. But none of the koalas showed transients between the old and the new time. However, there were transients in feeding from 14:00 to dusk in both koalas. In any case, weighing in the afternoon prevents interruptions in the morning, while activity bouts in the afternoon have already been more frequent before. This should increase well-being in the koalas.

Conclusion: Koalas in hands-off management do not react as strong to the keeper as those with frequent handling. Daily maintenance of the enclosure therefore has little impact on the activity pattern. Intensive contact on the contrary triggers activity during morning cleaning. However, frequently handled koalas resist less to handling and settle down easier. As shown in Vienna, handling in the morning interrupts resting times, which results in discomfort and possible stress. Thus, handling should take place during physiological activity times. This is also advisable for food introduction, because koalas fed in the afternoon reacted stronger to the fresh browse than koalas fed in the morning.

4.5 Koala Encounter - Influence of visitors

4.5.1 General activity pattern

On first examination, the ethograms of Koala Encounter are strikingly different from those at Koala Walkabout. Even so, a closer comparison reveals interesting similarities. The biggest differences between the two groups are three distinct feeding peaks at Koala Encounter during daytime. The koalas at Koala Walkabout rest at the same time. The three peaks are directly related to keeper's activity and the introduction of fresh browse. However, feeding activity at Koala Encounter increases again around the time of the Keeper's Talk at Koala Walkabout and remains high during the afternoon. The nightly peaks in the activity profile are surprisingly similar to those at Koala Walkabout. In both groups there is a peak between 20:00 and 21:00 and a lull between 02:00 and 02:30.

This conformance is particularly astonishing since the enclosures had no contact with each other and the data have been collected in different years. There were also no external events that could trigger activity at these times. Therefore, the feeding bouts in the afternoon and the nightly feeding pattern were very likely endogenously controlled. Also, in both enclosures entrainment to dusk and dawn is clearly visible.

The high feeding peaks during the day were always triggered by the introduction of fresh browse, but not the afternoon feeding at Koala Encounter. There are two possible explanations. First, visitors leave Koala Encounter at 15:00 and feeding increases slightly after that. It is thinkable that the koalas prefer to feed without visitors. However, there are still visitors in front of the enclosure and the onset of afternoon feeding bouts is not related to the presence of visitors in the bay itself. Also often feeding starts much later in the afternoon. Given the fact that the koalas at Koala Walkabout had an extended feeding bout in the afternoon and several of the koalas at Duisburg and Vienna showed increased feeding activity at that time, it is much more likely that the afternoon is the physiological time for koalas to feed. This also corresponds with the observations of feeding peaks in the afternoon in free-ranging koalas (Hoetelmans & Kregten 2003). Also, feeding at Koala Encounter again is related to dusk as clearly seen in the individual activity profiles and ethograms.

Fresh browse does not always trigger the same response at Koala Encounter. At 07:00 in the morning it is followed by slightly longer feeding bouts than later in the day. The PSTH shows the highest amplitude at this time. As already discussed for Koala Walkabout, the browse dries out over night and the good quality leaves have been consumed, so the stimulus at this time should be stronger than later on in the day. Feeding bouts at 11:00 were shorter than at 07:00 and koalas at Bay C did not always start feeding at this time. Even so, on some days there were feeding bouts between 11:00 and 13:00. At 13:00 feeding was actually rare at Bay C, and even at Bay B it was not as common as at 11:00. On several days there was still enough fresh browse, so the keeper would not provide more. Hence the stimulus for feeding was weak at 13:00. Therefore the stimulus at 13:00 might also overlap with the feeding triggered at 11:00.

There was no anticipatory activity visible at any of the food presentations, so it is very likely that the introduction of the fresh browse is no Zeitgeber but masks the activity rhythm. However, *Maggie* and *Georgie* showed patterns in feeding activity that could be interpreted as relative coordination between dawn (respectively nocturnal feeding activity) and the food introduction at 07:00. In this case there would be a direct influence of food on the pacemaker. But as in Vienna it is most likely within the physiological resting time of the koalas and therefore might even be a disturbance.

4.5.2 Influence of visitors

Visitors were allowed for a maximum of two hours in the enclosure for photo shooting. This was accompanied by a keeper who monitored the koalas for signs of stress. However, obvious stress symptoms like ear flapping, increased pellet production, vocalisation and aggressions towards visitors were seldom or never observed. For most of the photo session the koalas were resting and feeding. Locomotion was observed sometimes, but the koalas very rarely came to the ground. A pilot study at another part of Koala Encounter with other koalas has shown no significant differences between koalas involved in the photo session and those in the adjacent enclosure during the sessions .

For method discussion behaviour between 11:00 and 15:00 was observed with and without visitors. The ethograms showed no striking differences between days. There was usually a feeding bout at 11:00, then the koala rested, and in some cases there was a second bout at 13:00. Locomotion was rare at this time of day. There was also little difference in time budget. Koalas rested slightly more and fed slightly less during the sessions than on other days, but these differences were not significant. As a next step, time budget of the complete days were compared. Again the koalas rested slightly more, but the only significant difference was a reduction in locomotion.

If visitors act as a stressor or disturbance the behaviour of the koalas might not be altered for the actual time of contact, but there might be general differences to undisturbed koalas. The ethogram already showed that feeding in the morning might disturb the physiological resting times of the koalas. The visitors, who usually came very close to the koalas, moved food branches and talked next to the resting koalas, would even increase this disturbance. Therefore time budget was compared to Koala Walkabout. Koalas from both enclosures differed significantly. Koalas at Koala Encounter rested on average 16 hours 58 minutes, 1 hour 41 minutes less than those at Koala Encounter. That was the shortest resting time measured in this study and was considerably lower than the resting times of 18 to 22 hours reported for free-ranging koalas (Smith 1979a).

Four hours per day were spent with feeding. This was 1 hour 9 minutes longer than at Koala Walkabout and also fairly high compared to free-ranging koalas. Koalas at Koala Encounter had twice as much feeding bouts per day than the females at Koala Walkabout in summer. The average duration of a feeding bout was 10 minutes shorter than at Koala Walkabout and long bouts were rare. An extended bout as regularly observed during the Keeper's Talk has not been triggered by any of the food presentations at Koala Encounter. With an average duration of 21 minutes, feeding bouts were similar to those measured at Lone Pine Sanctuary, where koalas are kept in high density (Logan & Sanson 2003) and those reported from non-lactating females in the wild (Zoological Society of San Diego 2001; Yusuf & Rosenthal *unpublished data*), but longer than those at Vienna Zoo.

Intensive locomotor activity (Loc3) was more than five times higher at Koala Encounter and the koalas are three times more often on the ground. Presence and especially pacing on the ground can be a sign that something is wrong, including the presence of stressors or mishandling (Ellis *et al.* 1995). At Koala Walkabout these behaviours were mainly displayed during evening, night and early morning, so the keepers were seldom able to observe them. Increased locomotor activity would result in higher energy requirements. Koalas have little fat reserve (Cronin 1987), so an increase in energy requirements needs to be answered by an immediate increase in food intake. This can explain the longer feeding times at Koala Encounter. However, due to the toxicity of eucalyptus leaves and the swelling of gut content in the caecum (Wood 1978; Obendorf 1983), koalas can only increase their food intake to a certain amount. Female koalas in such a situation would not have enough energy for breeding and might suffer from health problems and eventually death (Cronin 1987).

The increased demands of food intake and the high amount of time spent with locomotion also severely reduce the resting time of the koalas. No qualitative data on resting were collected in this study, so it is not clear how much of the time is spent sleeping. However, during photo sessions koalas have often been observed to rest motionless with eyes slightly open (*pers. obs.*, *pers. comm.* from various keepers). It is not known if this behaviour is displayed without humans in the enclosure. This behaviour might not be effective resting, but some kind of "defensive sleep" as observed in cats (Pfleiderer 1990). Active koalas attracted more attention from the visitors and where used for photos more often. Movement was also often acknowledged with exclamations by the visitors. Inactivity might actually establish a quieter atmosphere during the photo sessions. Therefore, koalas would rest during this time, but be watchful and tense.

The differences in the ethograms are also reflected in the day:night ratios. Although the koalas at Koala Walkabout rested only slightly more during daytime, there was a severe difference in feeding. At Koala Walkabout, feeding was more often observed during the day, while at Koala Encounter, there was no difference between day and night. As seen in the ethograms this is not due to frequent feeding, but to the three peaks when fresh browse was presented. Locomotor activity was also more often observed during the day at Koala Encounter and the koalas were significantly more often on the ground. Hence, the koalas at Koala Encounter were generally more diurnal than their specimens at Koala Walkabout.

Conclusion: Overall, the differences in activity pattern and time budget and the direct observations suggest that well-being at Koala Encounter is lower than at Koala Walkabout. For once, there *is direct disturbance by the keepers and visitors during sessions during the physiological resting time. Additionally koalas show stress signs (high locomotor activity on the ground) at night. These stress signs resulted in higher activity and therefore higher energy demands and reduced resting time. This again reduces well-being. The results also show that visitors have a negative influence on the koalas which might not be detectable by direct observation during contact, but at other times of day.*

4.6 Increased locomotor activity

At Koala Encounter locomotor activity was not constant, but changed during the time of observation. *Cooee* and her yearling daughter *Coco* had the highest locomotor activity at Koala Walkabout. From 12 January on locomotor activity was very high in *Cooee* and she was on the ground more often than before. At the same time locomotor activity increased in *Coco* and often both koalas were moving in the same observation interval. Locomotor activity was reduced again on 23 January in *Cooee*, but remained high in *Coco*.

At this time, *Coco* was 13 months old. Koalas are weaned with about 12 months of age (Smith 1980c), but *Coco* still suckled regularly. *Cooee* always tried to prevent her from doing this. This resulted in a squabble, during which *Cooee* tried to scratch and bite her daughter into the neck. Usually *Cooee* then retreated after a few minutes, followed by *Coco*. In several cases *Coco* finally succeeded and was allowed to suckle. Another problem was that *Coco* still tried to ride on her mother's back. *Cooee* tried to prevent that too. So *Cooee* often moved away to avoid her daughter's approaches and was followed by *Coco* through the enclosure. Hence, there was increased locomotor activity.

The female *Carla* was transferred to Bay B in exchange for another female and her joey. Locomotor activity then generally increased in *Maggie* and *Carla* and long bouts of locomotion on the ground were observed in *Maggie*. After ten days, locomotor activity was reduced in *Carla*, after 16 days in *Maggie*.

Within the first eight days, *Maggie* often moved away from *Carla*, when *Carla* came close. Also, two minor fights were observed between the two on 6 January and 9 January. Later on, *Maggie* did not move away any longer and no fighting was observed. Therefore, the increased locomotor activity was probably a result of tensions between the two koalas. After two weeks they had adjusted to each other and there was less need for avoidance behaviour. The koalas settled down.

On 25 January locomotor activity again increased in *Maggie*, but not in *Carla*. In *Georgie* locomotor activity increased on 7 January without correspondence to the other two koalas in the enclosure. Since the observations are made during breeding time, this might be a sign for oestrus behaviour, which can involve increased locomotor activity in the females (1980c). Similar behaviour has been observed in Duisburg and Vienna, but not at Koala Walkabout. Smith (Cronin 1987; Sharp 1995) states that oestrus behaviour is rarely seen, since it is either brief or a male responds immediately. Only at Koala Walkabout a male had immediate access to the females. This male approached the females frequently during breeding season, without any conspicuous behaviour detected by the observer, and in several cases mated with her. In Duisburg and Vienna the keepers decided when to allow contact between the male and one female. At Koala Encounter no breeding was scheduled for the ongoing season and there was no male available for the females. This inability to mate might result in increased locomotor activity. It has been suggested that in the wild, female koalas actively approach males and even cover long distances for mating (Morris 1964; Smith 1979a). To verify this hypothesis, hormonal levels should be assessed in females with high locomotor activity.

Conclusion: Increased locomotor activity has been proven to be related to problematic situations in koalas. Although it was not always possible to find the cause of this increase in this study, locomotor activity is a promising parameter for the assessment of stress and should be tested in combination with other physiological parameters, e.g. glucocorticoid levels, heart rate.

4.7 Chronoethology – a tool to evaluate well-being?

Captive koalas rarely show stereotypical behaviour as known from other zoo animals under strain (Wood 1978). There is a number of stress signals (Carrick *et al.* 1990; von Holst 1998), but it seems they are not satisfying for a proper assessment of well-being (Logan & Sanson 2002b). One major method to monitor health state in captive koalas is weighing. However, this study has shown that weighing can be a disturbance and hence even a stressor itself. Therefore a further, non-invasive method is needed.

The observation at Koala Walkabout, Taronga Zoo has shown that activity patterns of koalas are constant throughout the year and appear to be similar in a group under natural light regime and with little interference by keepers. They also showed that activity pattern and time budget in these conditions were comparable to those of free-ranging koalas. The ethograms obtained at Koala Walkabout therefore fulfil the requirements of a "reference-ethogram" for captive koalas. These ethograms also showed that in captivity light might not be the strongest Zeitgeber, but can be overridden by food.

The comparison of activity patterns between Taronga Zoo and the two zoos in Europe have shown that the husbandry guidelines provided by San Diego Zoo lack adjustment to endogenous rhythms. Handling at physiological resting times to increase activity and the animal's attractiveness to the visitors results in reduction of well-being (also see Gattermann & Weinandy 1997). This study has shown that koalas reacted stronger to a stimulus given at a physiologically adequate time (food introduction in the afternoon). However, an increase in activity is related to an increase in energy requirements and therefore food intake (Ullrey *et al.* 1981b; Logan & Sanson 2002a). Since the food of the koala is low in protein but contains potentially toxic essential oils and tannins, higher food intake would result in higher strain for the digestive system. Based on this, koalas are expected to cope poorly with an increase in foraging effort (Cork et al. 1990; Hume & Esson 1993). Hence, activity levels should stay within the natural range of a species and physiological resting periods should not be disturbed.

Unfortunately no parameters were found to identify health problems in koalas. However, changes in locomotor activity have been associated with social strain and possibly with oestrus. Having said this, chronoethology turned out to be a promising tool to assess general housing conditions. It was possible to identify stimuli influencing the activity pattern of captive koalas and, furthermore, to decide upon advisable times for handling. I was able to show in this study that visitors have a severe influence on activity pattern, which is neither detectable if only a short part of the day is observed, nor if observation is reduced to the koalas in questionable conditions. Therefore chronoethology gives valuable information on the live-situation of an animal and helps to identify the cause of possible issues.

Conclusion: Chronoethology has been successfully used to assess general housing conditions. Comparison of activity patterns between koalas has shown to which extend husbandry and handling interferes with endogenous rhythms and which times are suitable for handling. Locomotor activity has been shown to act as a parameter for discomfort and stress. So far the use of chronoethology is not established as a physiological stress assessment related to hypothalamic-pituitary-adrenal activity. Nevertheless, interruptions and changes of rhythms as well as influences on the pacemaker can be detected and conclusions on well-being and physiological state can be made. Further research will examine to which degree such changes in rhythmicity are coupled to hormonal activity.

4.8 Resting location

Most of the time in koalas is spent resting. Koalas are arboreal animals and seldom leave trees. Although koalas are often observed resting in food-trees, they also use non-food trees (Lee & Martin 1988; Moeller & Grzimek 1988). Based on this, it can be expected that captive koalas would prefer living trees to bare trunks as resting place too.

Trees were only available at Koala Walkabout and at Duisburg Zoo. At Koala Walkabout there were clear seasonal and individual differences in the use of the tree. The females spent an average of 52% of their resting time in the tree, mostly in the canopy. Values were higher in winter, where the females spent 56% of the resting time in the canopy and 9% on the trunk. During the day, at least one, often both females were seen in the canopy, and at night the tree was still regularly used. One preferred spot of the females was at eye level with the visitors and almost reachable by hand. However, the females spent a considerable amount of daytime there. *Ken* on the other hand was rarely seen in the canopy, especially at daytime, but was regularly observed on the trunk. Ninety percent of his resting time was spent on one of the dead trees. In summer the single females spent slightly less time in the canopy than in winter. There was less often a female in the canopy and almost never more than two. Instead, the trunk was more frequented than in winter. Again *Ken* was rarely seen in the canopy, but regularly on the trunk. Generally *Ken* seemed to prefer the dead trunks. However, he only rested in the tree, when no or few females were there. Since he frequently retreats from the females it is possible that he avoids the canopy because of the females' presence.

In Duisburg, the male *Kambara* spent 24% of his time in one of the two fig trees, in summer more time than in winter. He used the tree mainly at night and, in summer, in the morning. The females had only one fig tree, which was almost exclusively used by *Allora* in summer and sometimes by the juvenile *Koomela* in winter. *Kangulandai* and *Yuri* rarely used the tree. *Allora* spent a considerable part of the day in the tree, especially in the morning and early afternoon. She was the youngest female in the group and had been transferred to the enclosure in September 2002. While *Yuri* and *Kangulandai* often sat next to each other, *Allora* usually stayed apart from the others. She also was more reserved towards the keepers. It is most likely that she used the tree for hiding.

The husbandry guidelines for the San Diego loan programme advises that only defoliated wood has to be taken for furnishing and foliage re-growth has to be removed for fear of poisoning. There have been cases of poisoning in captivity when a high amount of young leaves and shoots have been fed by the keepers (Cronin 1987; Lee & Martin 1988). However, living trees are common in Australian zoos and wildlife parks. Koalas have not been observed to feed on living branches during the study and no case of leaf poisoning has been reported from Taronga Zoo or Duisburg Zoo. Koalas are known to be very particular in their choice of leaves, so it is unlikely that the koalas will feed on poisonous leaves while enough good quality browse is available .

Conclusion: The study shows that living trees indeed were preferred resting site in some, but not all koalas. They provide natural shelter from visitors, other koalas and, in the case of outdoor enclosures, from the sun. None of the koalas has been observed to feed on the trees and no case of food poisoning has been reported for Taronga Zoo and Duisburg Zoo. Therefore it is recommendable to allow captive koalas access to a living non-food tree for sheltered resting.

For everything there is a season,
and a time for every purpose.
ECCLESIASTES

Chapter 5

Suggested changes in koala husbandry

Based on the results of this study and the discussion of related literature, a number of changes in koala husbandry seem advisable:

If koalas are kept in indoor enclosures, artificial light regime should have adequate Zeitgeber properties: if natural light is experienced by the koalas (e.g. through sky lights) the lights should be turned on and off close to natural twilight to avoid more than two changes in light intensity per day (see 4.3).

Day length in the natural distribution area of koalas has significant seasonal variations, especially in South Australia. At Taronga Zoo there was an obvious change in Zeitgeber strength and phase angle difference during the year, related to day length. Seasonal variations of artificial day length in Europe should therefore include more than one fixed day length in summer and one in winter (see 4.3).

Seasonal variations of day length in Europe are much bigger than in Australia. This is especially strong in summer, when European nights are considerably shorter than Australian ones. Since koalas are mainly nocturnal animals, it would be more useful to extend the summer nights artificially than the summer day (see 4.3).

The koala's reaction on fresh browse in this study was generally higher when it was introduced in the afternoon than when introduced in the morning. Even without fresh browse some koalas displayed increased feeding activity in the afternoon or evening. In free-ranging koalas, feeding peaks have been frequently observed at the same time. Therefore food introduction in the afternoon might be more natural than food introduction in the morning (see 4.1.1, 4.1.2).

The patterns of activity obtained in this study and those of body temperature measured by Degabriele and Dawson (1979) suggest that morning is the physiological resting time of koalas. Handling during physiological resting times can result in higher stress levels (Gattermann & Weinandy 1999; Wood 1978; Zoological Society of San Diego 2001) and should therefore be avoided (see 4.4.3, 4.4.4).

Handling often interrupts resting or feeding times in koalas, which might act as a stressor (Sharpe 1980). Though regular contact accustoms the koala to handling, koalas should not be weighed daily, but not more than once or twice a week (see 4.4.3, 4.4.4).

Even if no immediate stress symptoms are observed in koalas during visitor contact, this study has shown that it has an impact on activity pattern and time budget. It is therefore questionable, if the ban on touching koalas in New South Wales is enough to protect captive koalas or if visitor contact should be even more reduced. Actual contact between visitors and koalas is not advisable at all. For further assessment, physiological stress parameters should be analysed (see 4.5).

Twenty-four-hour video observation as being practiced by several koala holders should include chronoethological analysis with special emphasis on locomotor activity and reaction to external signals. Direct observation should not only cover daytime, but night time also, even more so since koalas are more active at night (see 4.5, A.3, 4.7).

As arboreal mammals, koalas usually rest in the canopy of trees. To avoid food poisoning, living plants are not permitted by the Zoological Society of San Diego. However, no case of food poisoning has been reported from one of the studied zoos, and koalas at Taronga Zoo and Duisburg Zoo spent a considerable part of their resting time in the living trees. Therefore, living non-food trees should be provided for natural shelter.

The real voyage of discovery consists not in
seeking new landscapes but in having new eyes.
MARCEL PROUST

Chapter 6

Summary

Koalas are popular zoo animals, but difficult in husbandry. In addition to their specialised diet of eucalyptus leaves, they are prone to "stress" and disease. Particularly in European zoos, the monitoring of their well-being has high priority and they are protected from possible stressors. However, stress signs in koalas are vague and monitoring techniques like weighing might result in discomfort itself. Additionally, husbandry routines are planned according to keeper's schedule, not to the endogenous rhythms of the koalas. Therefore it is necessary to investigate activity pattern in captive koalas and the signals influencing them. These signals have to be assessed on the strength and quality of their impact.

A total of 17 koalas have been observed in three zoological gardens in Australia and Europe. Koalas kept in outdoor enclosures with little human contact (Koala Walkabout, Taronga Zoo, Sydney) showed a uniform activity pattern, which was clearly entrained by light. Activity levels were higher during the night, and there was a pronounced resting period in the morning which corresponds with low body temperature measured by Degabriele and Dawson (1979). Activity peaks were related to twilight and changed during the year related to day lengths. However, there was a clear influence from the introduction of fresh browse which resulted in a distinct feeding peak in the afternoon. With short day lengths, this stimulus competed with dusk.

Activity patterns from koalas in indoor enclosures (Zoo Duisburg, Vienna Zoo) varied between individuals and in some cases lacked a detectable rhythm. Though activity peaks were related to light, entrainment to sunlight was weak. In winter, koalas reacted primarily to the artificial light, but some also showed activity peaks related to sunlight. Activity patterns in these koalas were less structured and differed severely from patterns expected according to literature. Activity was often related to the keeper's presence and food introduction. Frequency of feeding bouts was considerably higher at Vienna Zoo compared to the other zoos and the bouts were shorter in duration.

Time budgets of the koalas were within the range given in free-range studies . Feeding showed seasonal changes and was increased in lactating females. Koalas at Vienna Zoo had a high level of locomotor activity compared to the size of the enclosure.

Koalas at Koala Walkabout were not used to handling, so they resisted the keeper. The koalas at the two European zoos were handled regularly and settled down quickly. However, handling took place in the morning; in most koalas, there was no activity prior to it. In Vienna, resting periods were interrupted daily due to weighing.

Food introduction at Koala Walkabout took place in the afternoon. It was preceded by locomotor activity and triggered a long feeding bout in the koalas. It is not clear, whether food had true Zeitgeber properties or masked the endogenous rhythm. In the two European zoos, food was introduced in the morning. The peaks related to this were smaller than those at Koala Walkabout. Activity was rarely observed prior to food introduction.

The koalas at Koala Encounter, Taronga Zoo (Sydney), were regularly confronted with visitors, though no contact was allowed. Direct observation by the keepers did rarely show any stress signs. Activity patterns at night were strikingly similar to Koala Walkabout, but differed dramatically during the day. Food was introduced three times a day, which usually resulted in activity that interrupted a resting period. Generally, the koalas at Koala Encounter were more active than those at Koala Walkabout. They also displayed a high level of locomotor activity, especially on the ground, which is an accepted sign of discomfort in koalas (Wood 1978; Zoological Society of San Diego 2001; Yusuf & Rosenthal *unpublished data*).

In summary, this chronoethological study of the captive koalas showed that there are several problems with koala husbandry. Artificial light regimes for koalas are not sufficient for entrainment and result in unstructured activity pattern. This is especially the case in winter, when the day in Europe is artificially extended. Due to the mainly nocturnal behaviour of koalas, such an extension might not be necessary and therefore should be avoided.

Handling in Europe took place during the physiological resting time of the koalas. Interruptions of resting times are considered as stressors (Wood 1978) and should be avoided. Handling in the afternoon would be more suitable for the koalas and triggered activity in the two koalas at Vienna Zoo. It is also arguable if daily weighing is necessary to monitor health in captive koalas or if the frequent interruption of resting countervail the advantages of constant monitoring.

Frequent contact with visitors, even without the so-called cuddling, has a considerable impact on activity patterns and time budget of koalas, even if no immediate stress signs are displayed. Such contact should therefore be reduced to a minimum and chronoethological observations of the koalas should be used. A study on koalas with direct visitor contact is also advisable to revise the current legislation on "koala cuddling".

Koalas frequently rested in living trees if they had access to it. Since no food-poisoning has been reported from koalas using living non-food trees, the provision of living trees with an appropriate canopy should be included in the husbandry guidelines.

Increased locomotor activity has been shown to be related to conditions of discomfort or stress and possibly to oestrus. This is in accordance with literature (Wood 1978; Zoological Society of San Diego 2001). Further observation, combined with hormone analysis, are advisable to establish this parameter for evaluation of well-being.

Chronoethology has proven to be useful for the evaluation of husbandry conditions and group dynamics. Different to other, traditional ethological methods, it indicated problems and enabled me to advise more appropriate times for handling and food introduction. It is desirable that zoos already using 24-hour video observation include chronoethological aspects into their analysis.

Appendix A

Ethograms at Koala Walkabout, Taronga Zoo, Sydney

This appendix includes all ethograms of the koalas at Koala Walkabout. For the male Ken, data are plotted for one complete year. For the females Adori, Carrie and Yindi, most of the year is shown. Data gaps are visible for the periods in which these females were not in the enclosure. For the females Cooee, Felicity and Lowanna, ethograms are only plotted for the periods in which these individuals were kept at Koala Walkabout. See Table 2.1 and Fig. 2.1 for exact times.

A.1 Total activity

All figures show double-plotted chronoethograms. Green bars = feeding , red bars = locomotor activity; vertical blue line = morning cleaning, vertical green line = Keeper's Talk. Background colours: grey = night, yellow = twilight.

Fig. A.1: Feeding and locomotor activity in the females Cooee, Felicity and Lowanna during their time at Koala Walkabout.

In all females frequent activity bouts have been observed during the night. Activity ended during dawn and was low in the morning. There was a band of activity at 14:30 (Keeper's Talk) and at dusk.

Ethograms of total activity for Ken, Adori, Carrie and Yindi are shown in 3.

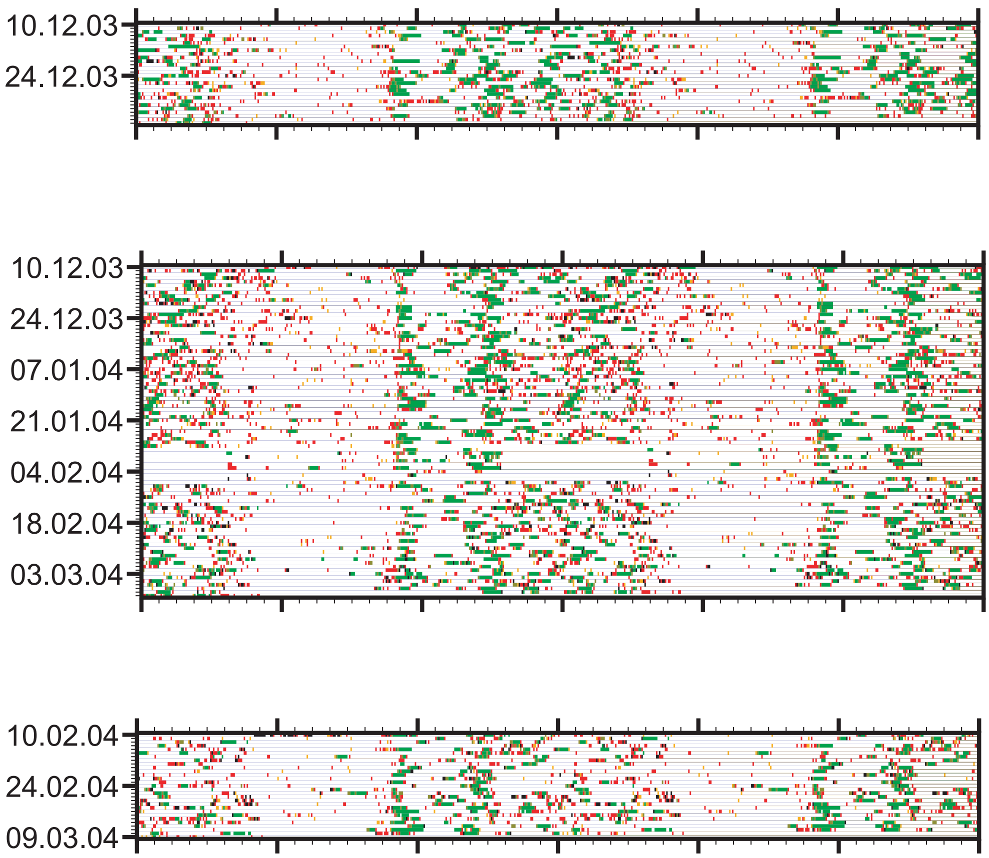

Figure A.1: Total activity in the females Cooee, Felicity and Lowanna during their time at Koala Walkabout. For further details see A.1

A.2 Feeding

All figures show double-plotted chronoethograms. Black bars in the ethograms indicate feeding, vertical blue line = morning cleaning, vertical green line= Keeper's Talk. Background colours: grey = night, yellow = twilight.

Fig. A.2: Feeding in the male Ken for one year.

Feeding began with a clear band at the Keeper's Talk. Several feeding bouts followed during the afternoon and night, related to dusk in autumn and spring. Feeding bouts ended prior to dawn. Generally more feeding has been observed in winter. Almost no feeding has been observed during the morning, feeding bouts increased after 12:00.

Fig. A.3: Feeding in the female Adori for one year.

Most feeding bouts have been observed during the night, ending at dusk. Little feeding has been observed during the morning. After 12:00 feeding increased and displayed a strong band at the Keeper's Talk.

Fig. A.4: Feeding in the female Carrie for one year.

Most feeding was observed during the night, ending at dawn. There has been little feeding in the first part of the day, until a strong band was displayed at the Keeper's Talk. This band was weaker than in Adori or Ken. No band was visible at dusk.

Fig. A.5: Feeding in the female Yindi for one year.

Almost all feeding has been observed during the night. There was a clear band at dusk, and feeding ended with dawn. Almost no feeding has been observed in the morning. At the Keeper's Talk, a clear band was only visible in summer.

Fig. A.6: Feeding in the females Cooee, Felicity and Lowanna during their time at Koala Walkabout.

During the night frequent feeding bouts have been observed. Feeding ended with dawn and was rare in the morning. In all three females there was a clear band at the Keeper's Talk and a second one at dusk.

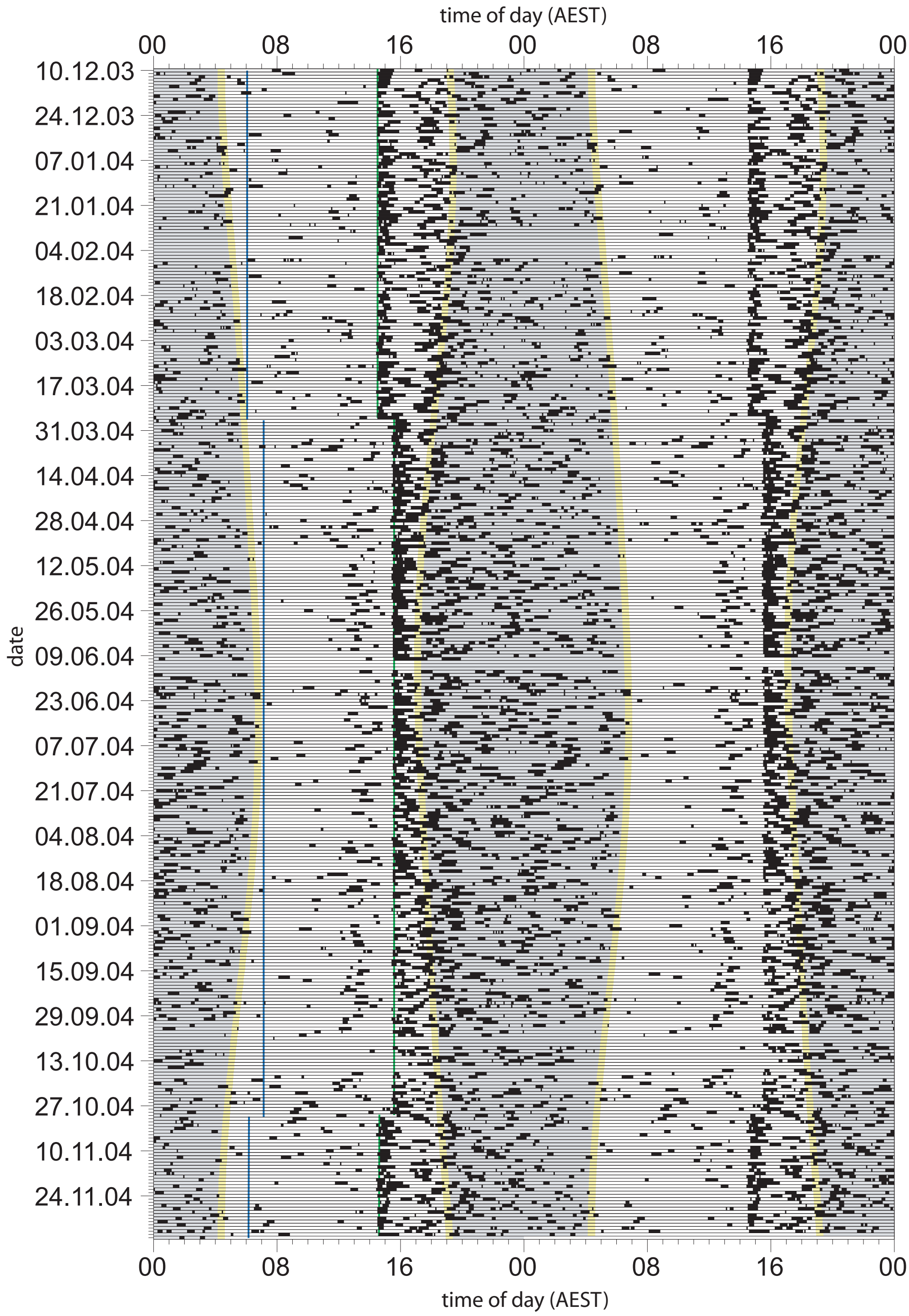

Figure A.2: Feeding in the male Ken for one year.
For further details see A.2.

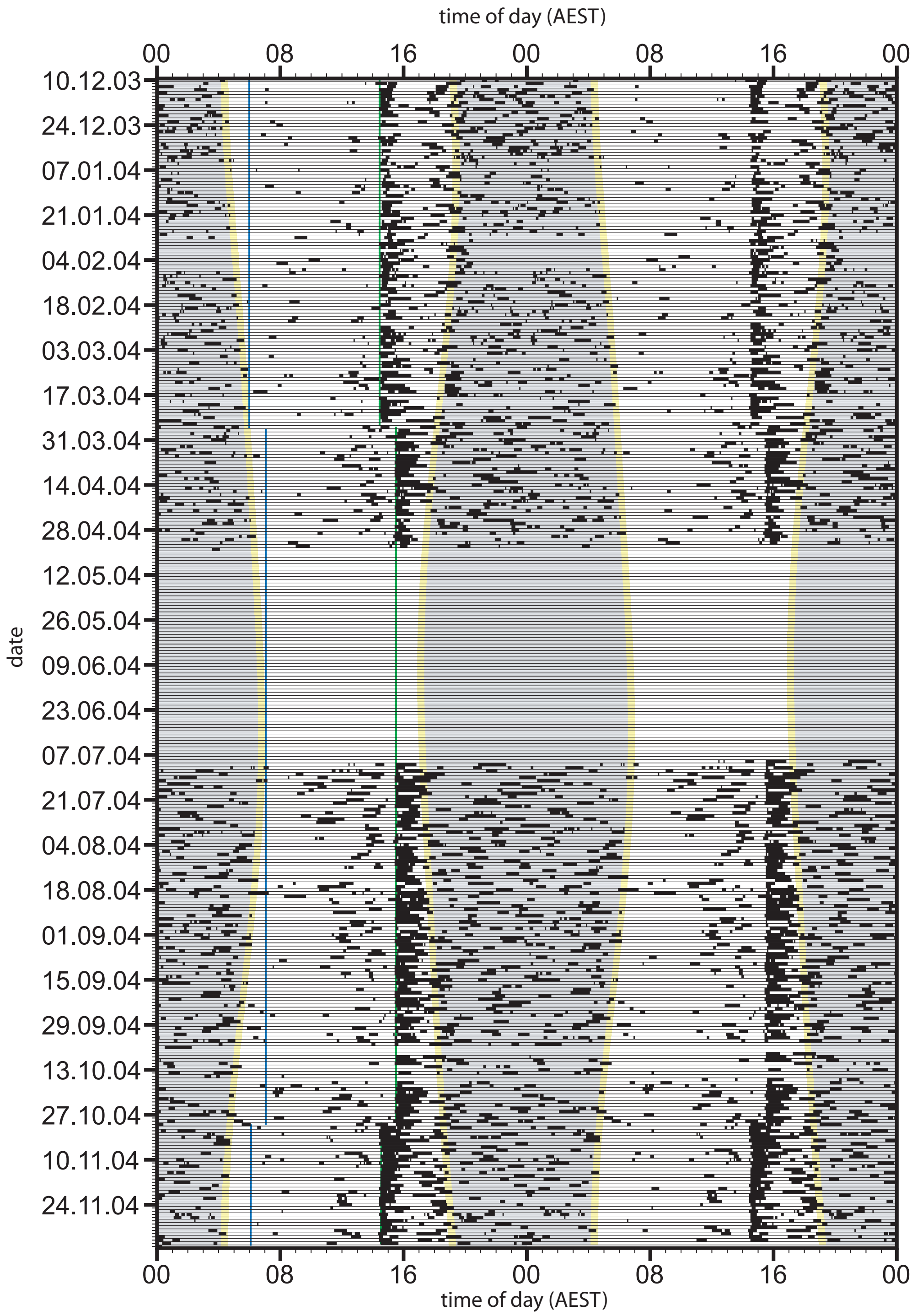

Figure A.3: Feeding in the female Adori for one year.
For further details see A.2.

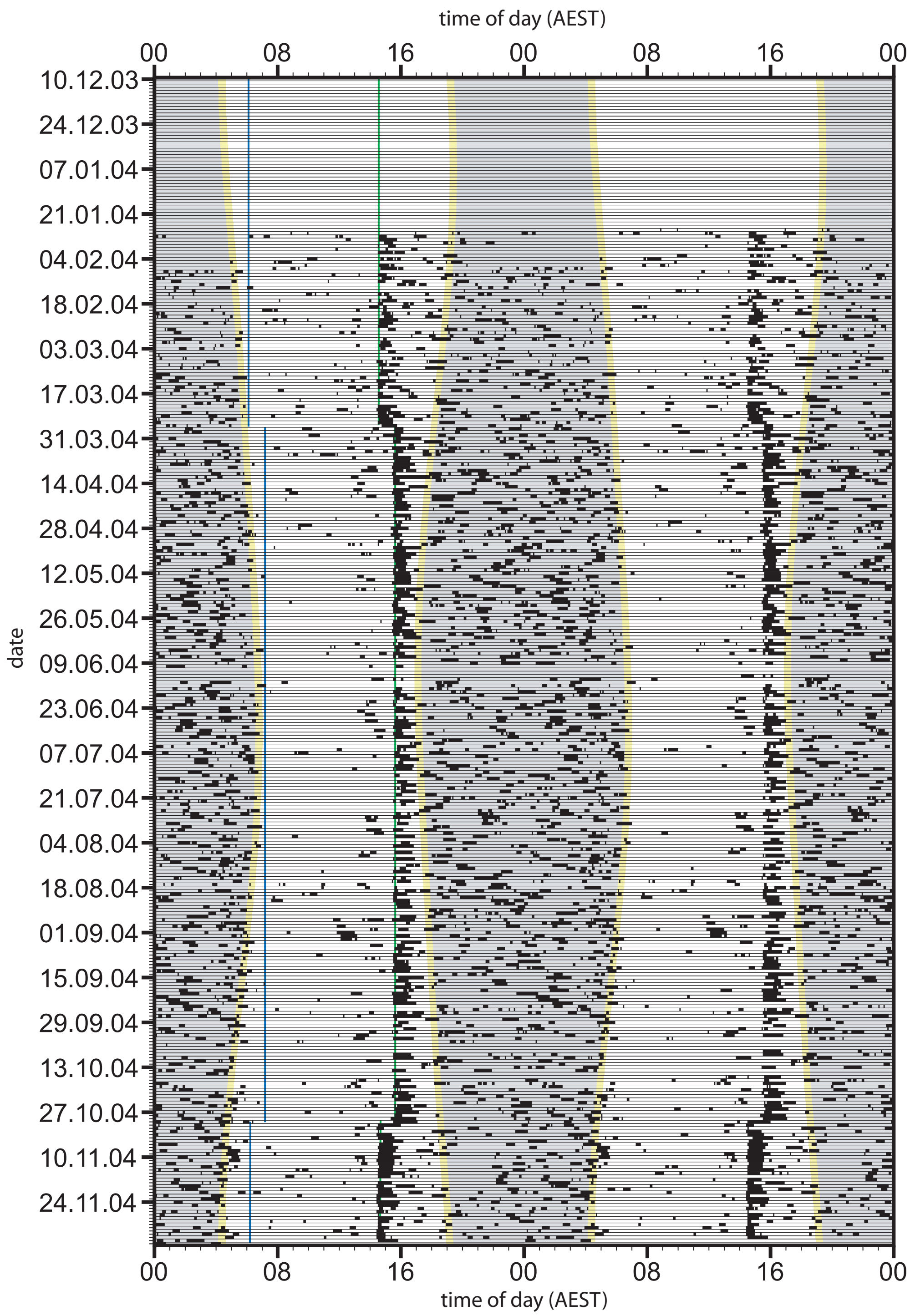

Figure A.4: Feeding in the female Carrie for one year.

For further details see A.2.

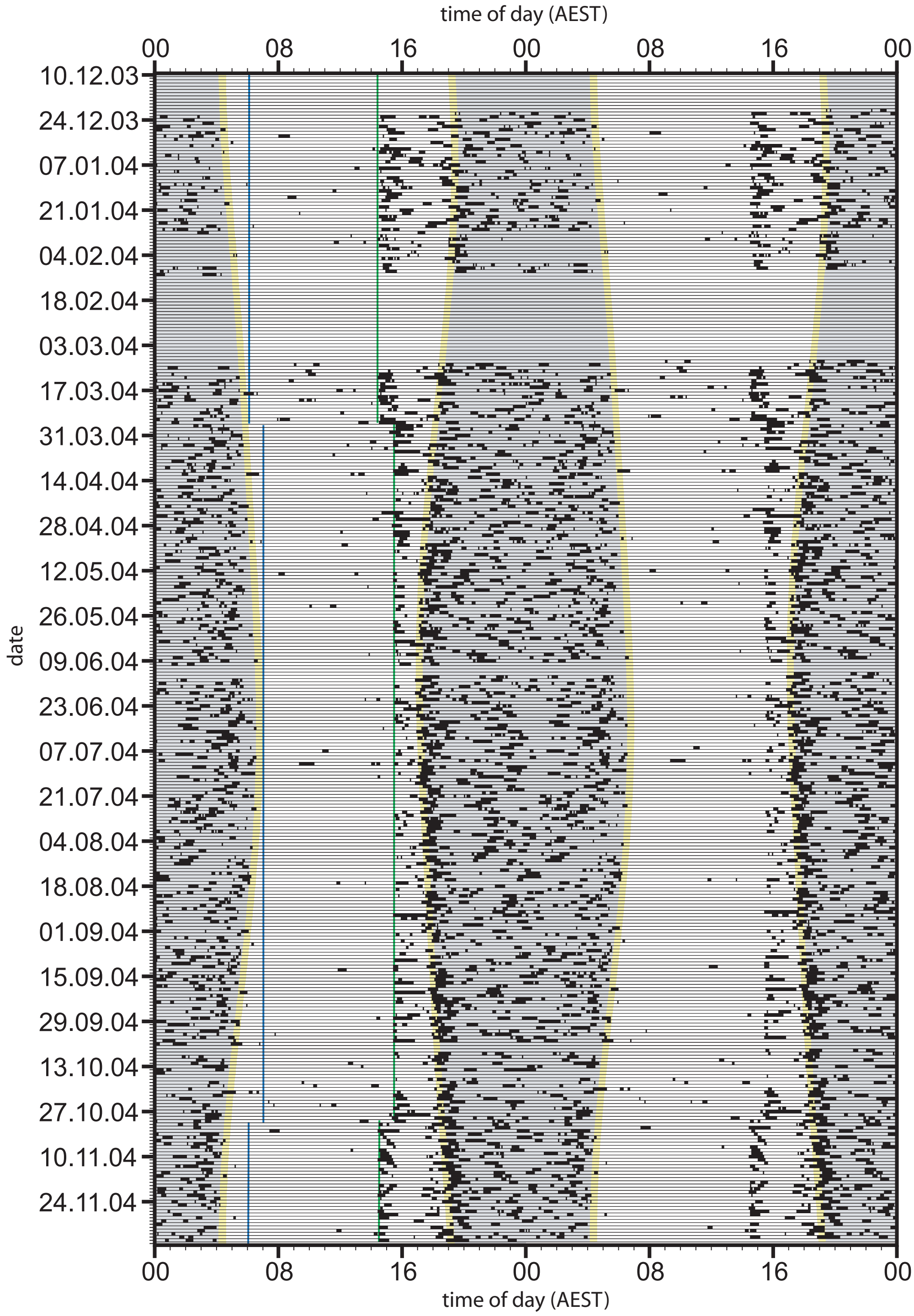

Figure A.5: Feeding in the female Yindi for one year.

For further details see A.2.

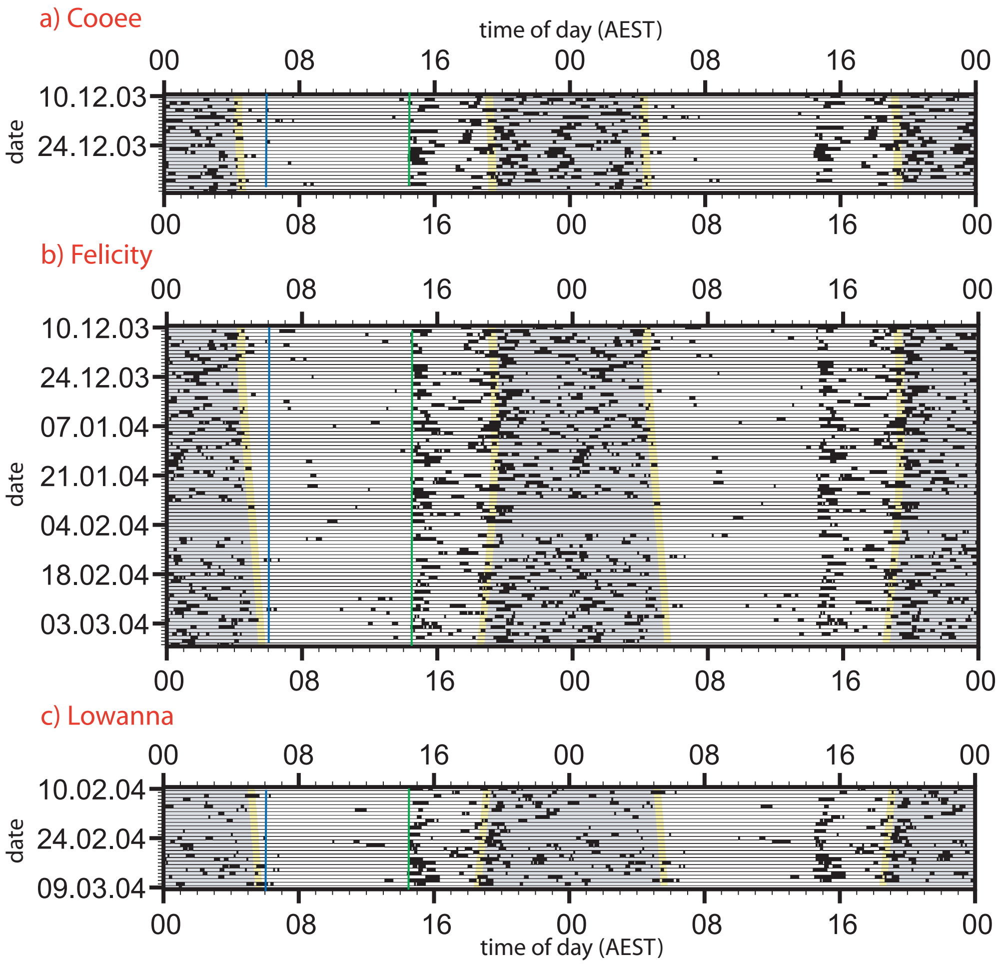

Figure A.6: Feeding in the females Cooee, Felicity and Lowanna during their time at Koala Walkabout. For further details see A.2.

A.3 Locomotor activity

All figures show double-plotted chronoethograms. Colours indicate levels of locomotor activity: orange = loc1, red = loc2; black = loc3; vertical blue line = morning cleaning, vertical green line= Keeper's Talk. Background colours: grey = night, yellow = twilight.

Fig. A.7: Locomotor activity in the male Ken for one year.

In the morning there was little locomotor activity, particularly in winter. It increased in the afternoon and displayed an irregular band of around the Keeper's Talk. In summer there was frequent locomotor activity in the afternoon, in the remaining year this was only the case at night.

Fig. A.8: Locomotor activity in the female Adori for one year.

Locomotor activity in the morning was low. There was an irregular band of locomotor activity around the Keeper's Talk. In the afternoon and night there was frequent locomotor activity, but this decreased at dawn.

Fig. A.9: Locomotor activity in the female Carrie for one year.

Locomotor activity was more frequent during the night and rather rare in the morning. There was an irregular band of locomotor activity around the Keeper's Talk.

Fig. A.10: Locomotor activity in the female Yindi for one year.

Locomotor activity was frequent during the night with another band at dawn. It was also high during early morning in spring. Particularly in winter locomotor activity was low during the day. There was a band of locomotor activity around the Keeper's Talk, but it was not as strong as in the other koalas.

Fig. A.11: Locomotor activity in the females Cooee, Felicity and Lowanna during their time at Koala Walkabout.

Generally locomotor activity was more common during the night. Around the Keeper's Talk, there was a clear band of locomotor activity, especially in Felicity.

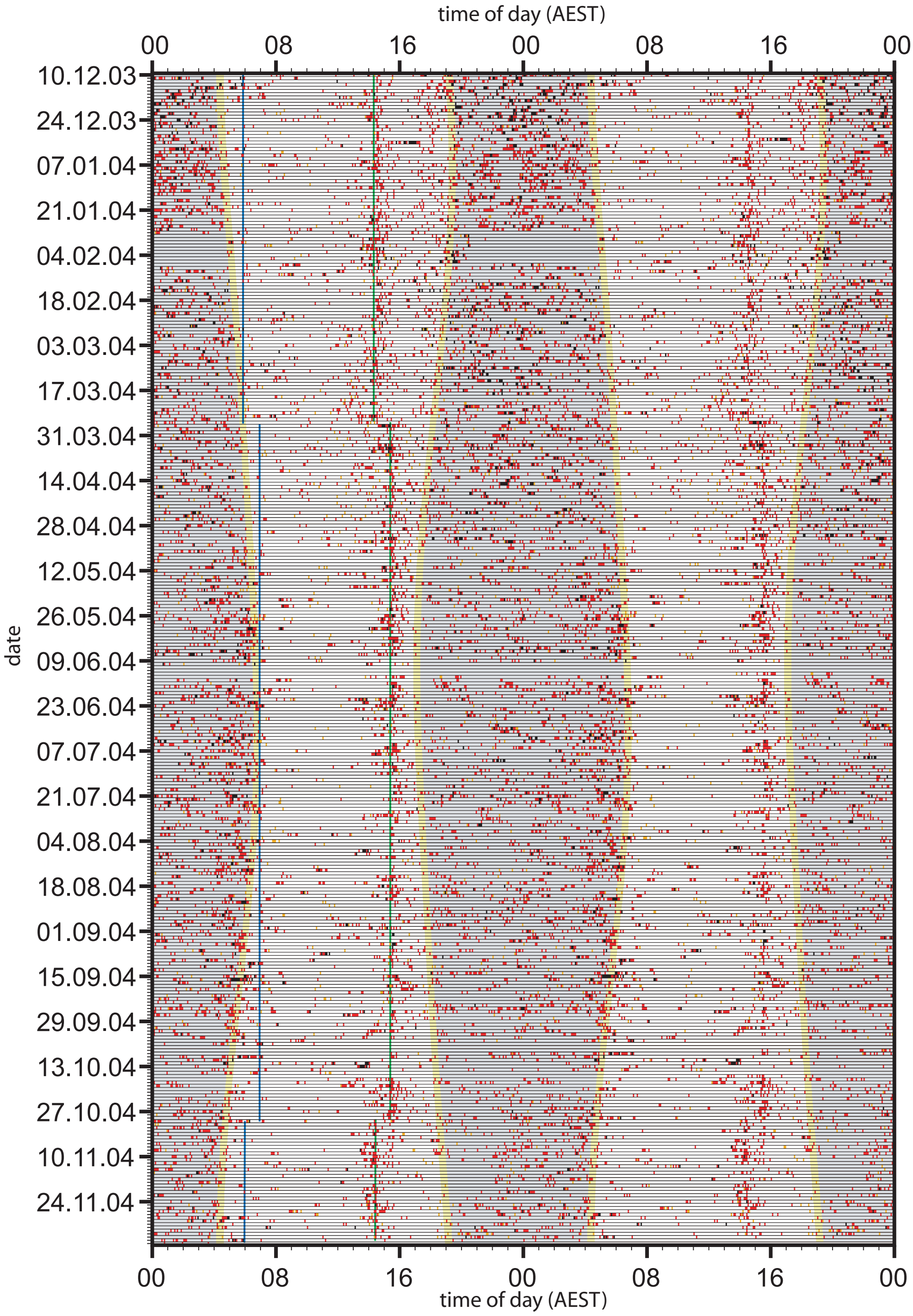

Figure A.7: Locomotor activity in the male Ken for one year.

For further details see A.3.

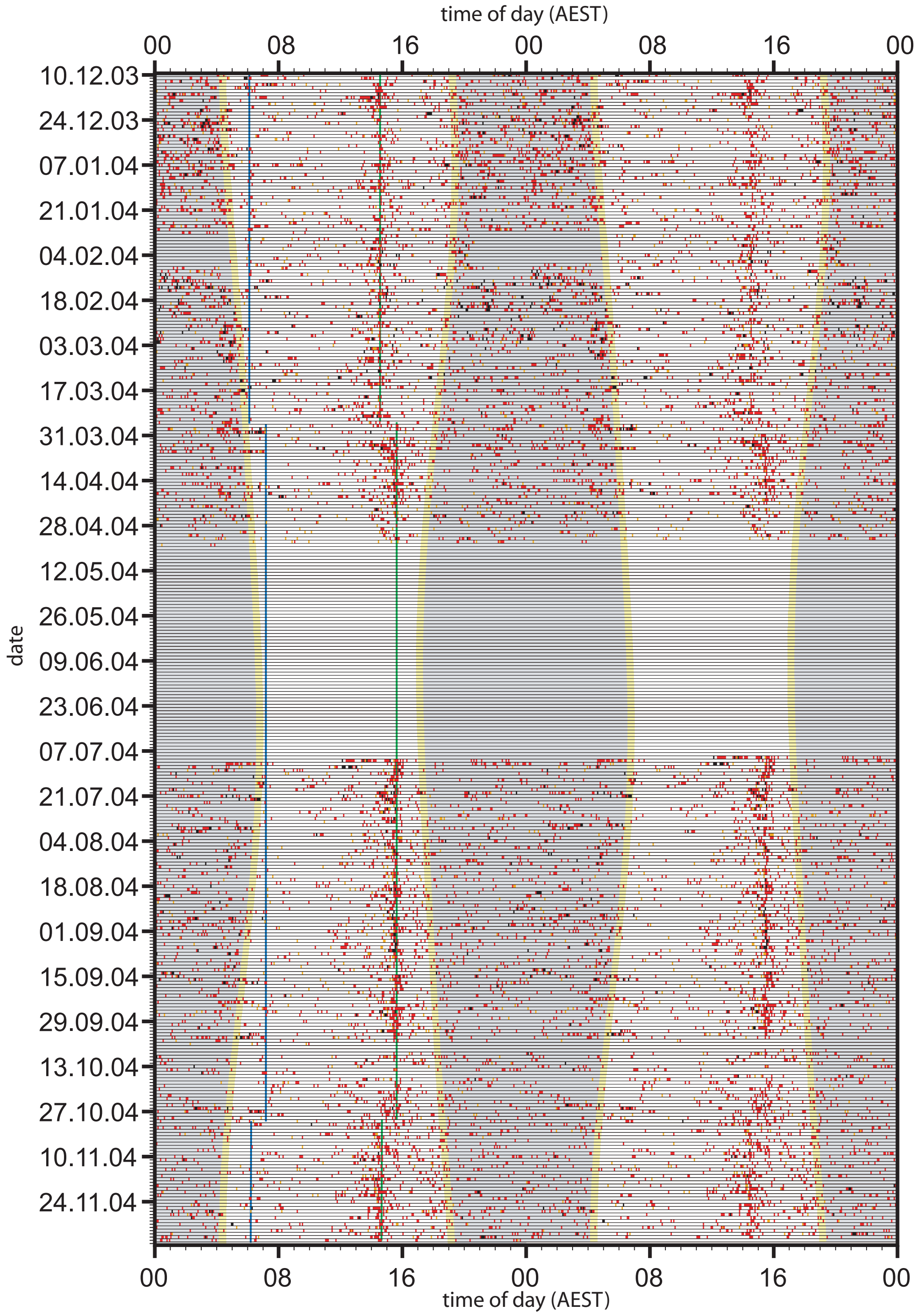

Figure A.8: Locomotor activity in the female Adori for one year.

For further details see A.3.

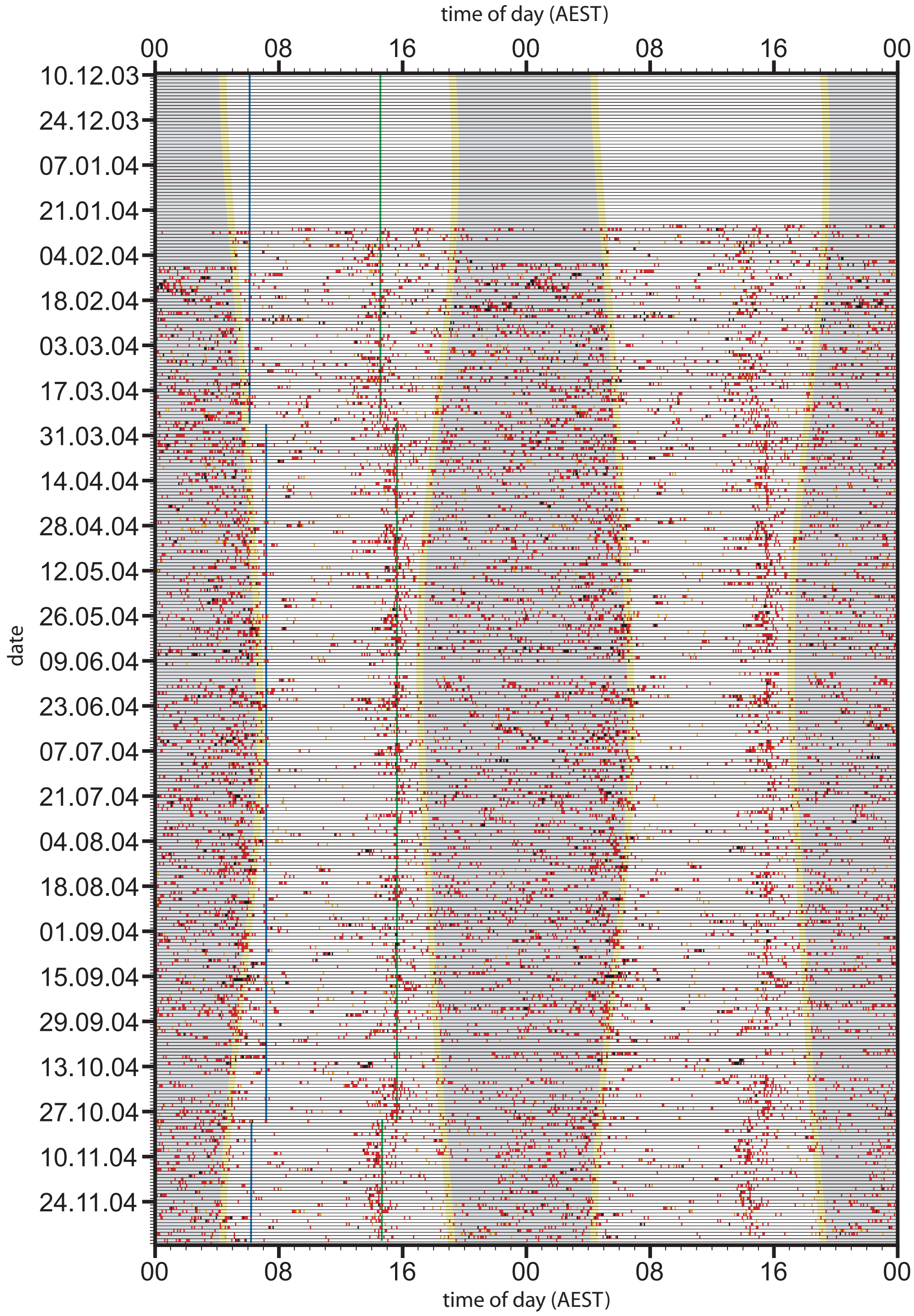

Figure A.9: Locomotor activity in the female Carrie for one year.

For further details see A.3.

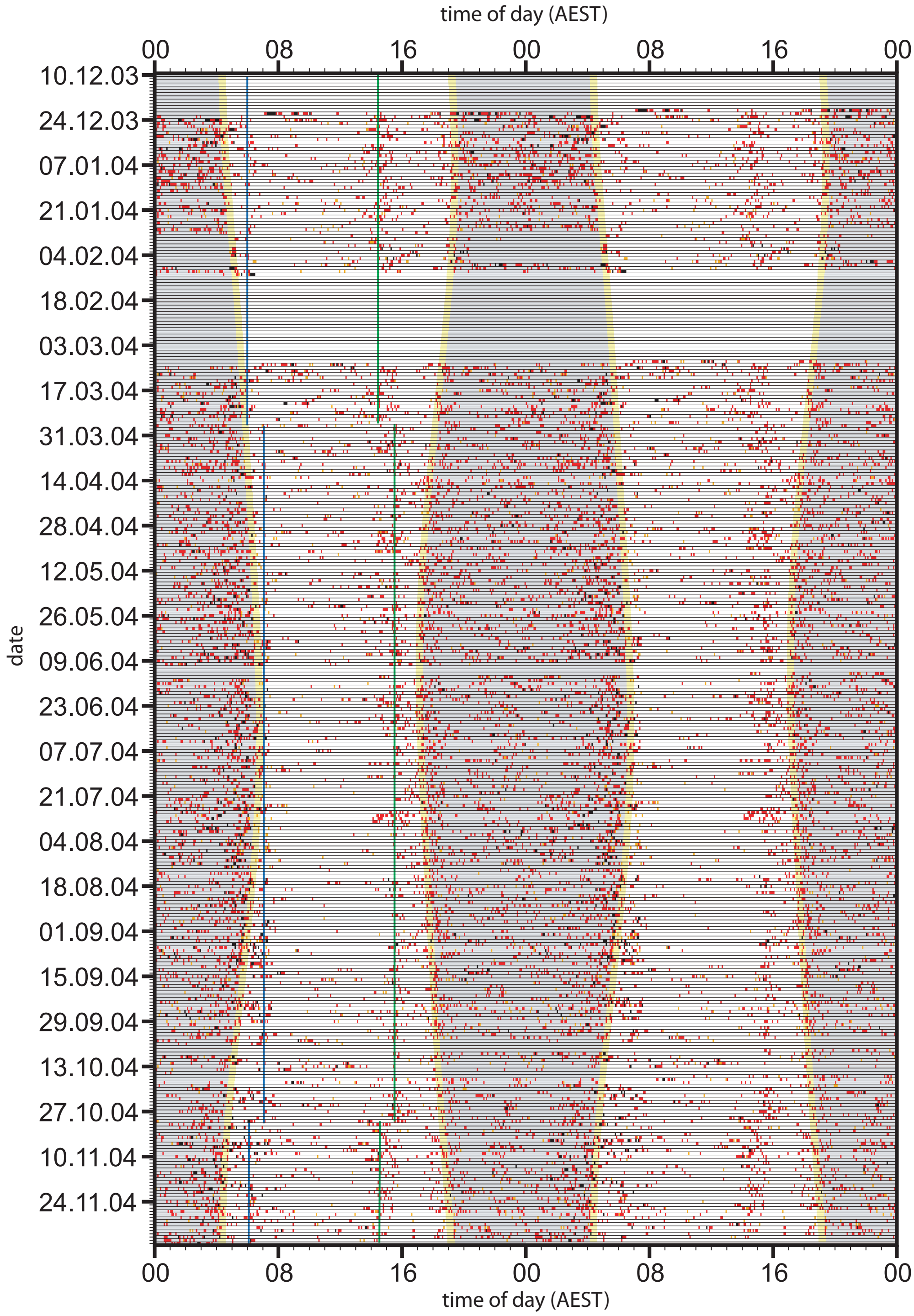

Figure A.10: Locomotor activity in the female Yindi for one year.

For further details see A.3.

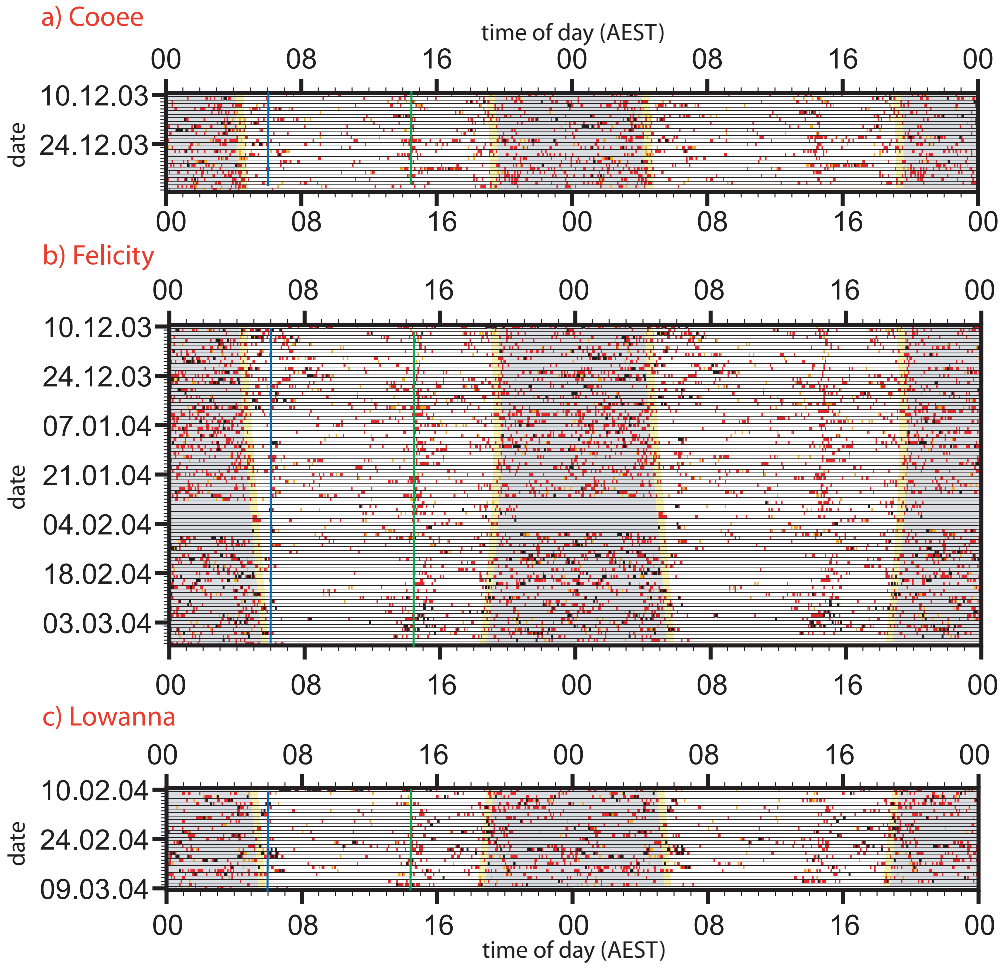

Figure A.11: Locomotor activity in the females Cooee, Felicity and Lowanna during their time at Koala Walkabout.

For further details see A.3.

A.4 Presence on ground

All figures show double-plotted chronoethograms. Black bars indicate presence on ground; vertical blue line = morning cleaning, vertical green line= Keeper's Talk. Background colours: grey = night, yellow = twilight.

Fig. A.12: **Presence on ground in the male Ken for one year.**

Ken was most often on the ground during the night. He rarely came to the ground in the morning, but there was a clear band prior to the Keeper's Talk. On one day, 13 October 2004, Ken sat on the ground in the shade of the Pittosporum tree for 3h 50 min. This was the hottest day of this summer, reaching its maximum temperature of 38.2°C at around 16:00.

Fig. A.13: Presence on ground in the female Adori for one year.

Adori was more often on the ground during the night than during morning. She also came to the ground regularly prior to the Keeper's Talk. This was stronger in winter.

Fig. A.14: Presence on ground in the female Carrie for one year.

Carrie was slightly more often on the ground during the night than during the morning. There also was a very weak band around the Keeper's Talk.

Fig. A.15: Presence on ground in the female Yindi for one year.

For most of the year Yindi was very rarely on the ground during the day and more regularly during the night. In October and November, Yindi was on the ground regularly in the late hours of the night and in the morning until 08:00.

Fig. A.16: Presence on the ground in the females Cooee, Felicity and Lowanna during their time at Koala Walkabout.

The females were very rarely on the ground during the day. There was a very weak concentration in the afternoon, around the Keeper's Talk.

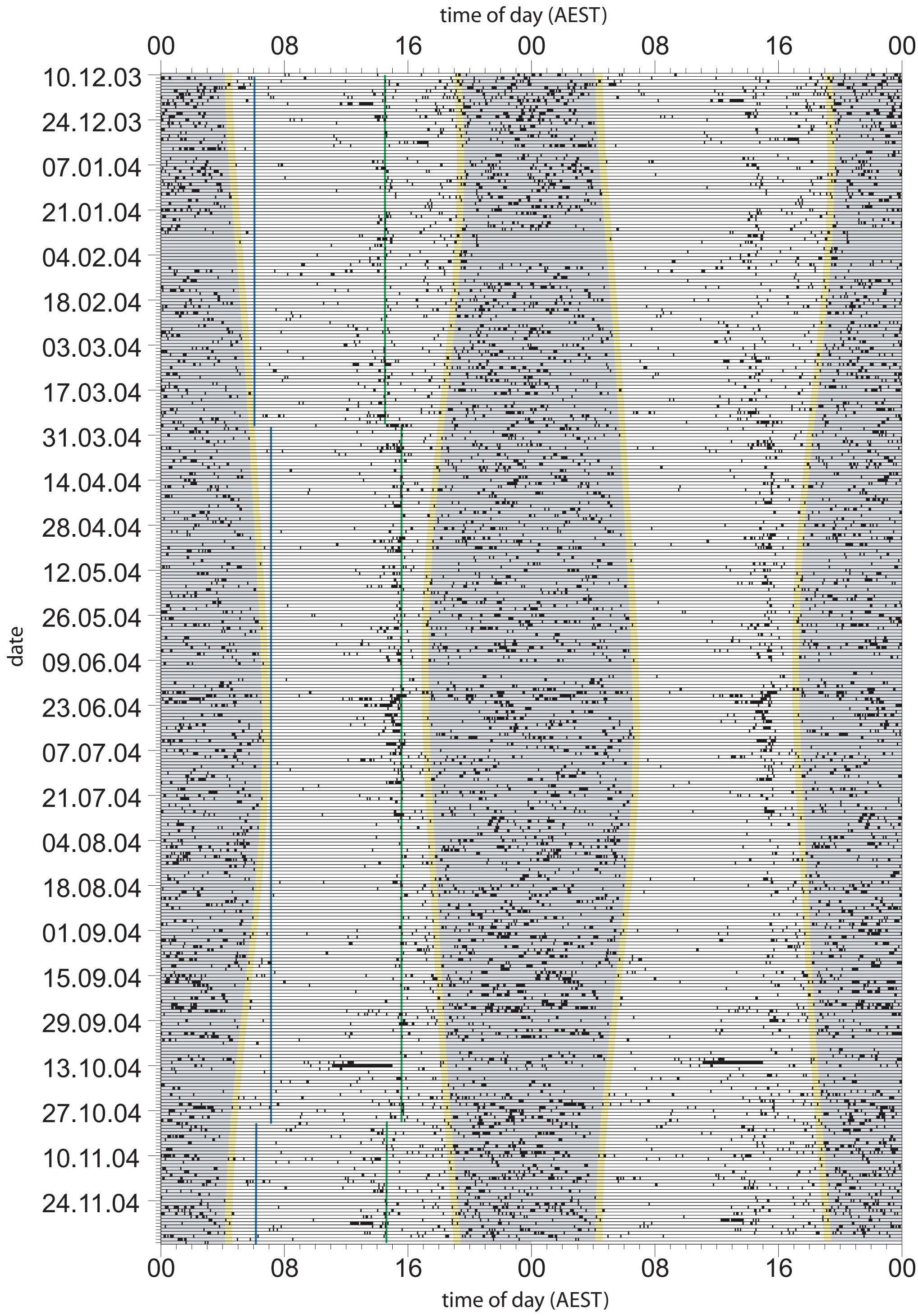

Figure A.12: Presence on ground in the male Ken for one year.
For further details see A.4.

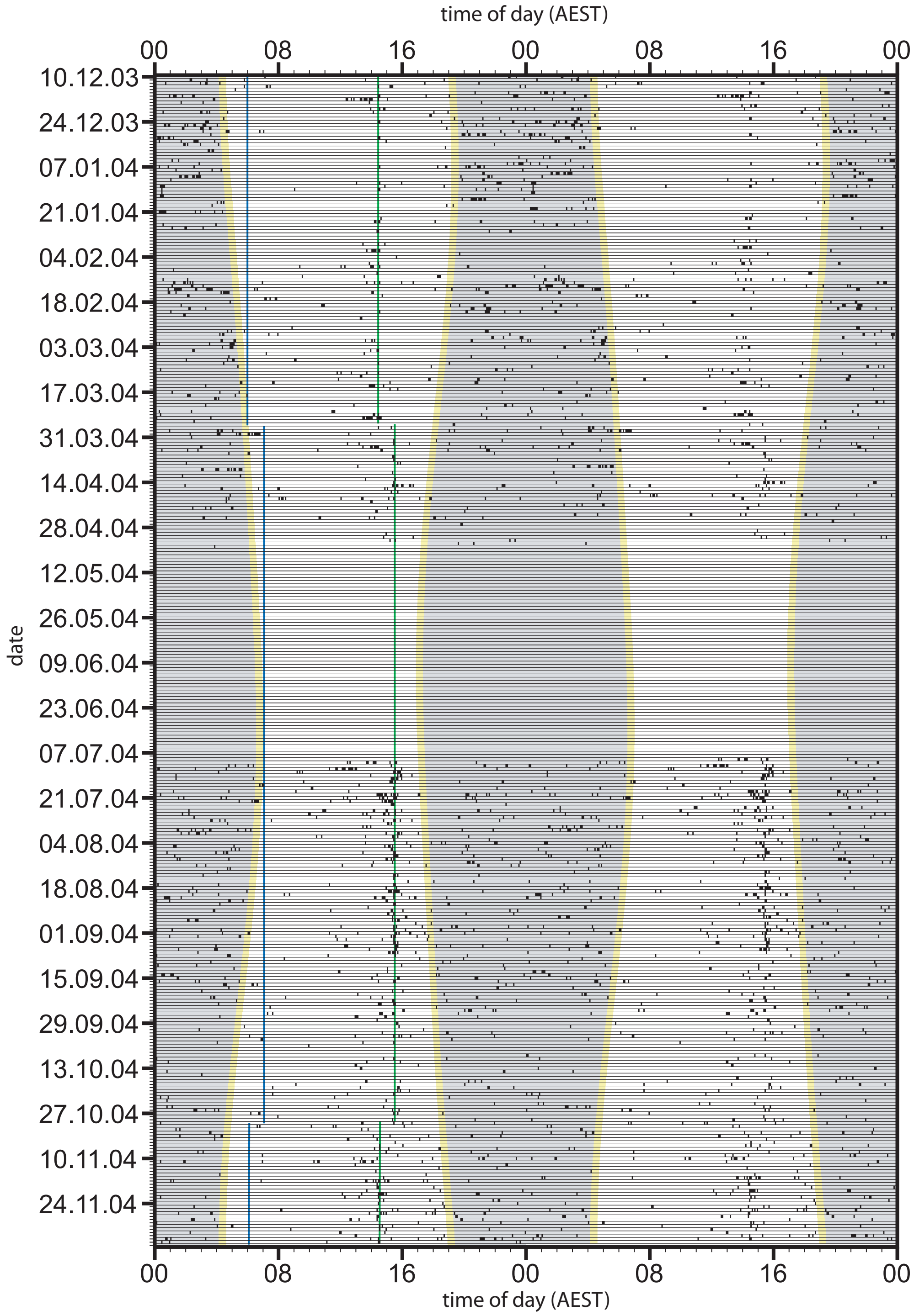

Figure A.13: Presence on ground in the female Adori for one year.

For further details see A.4.

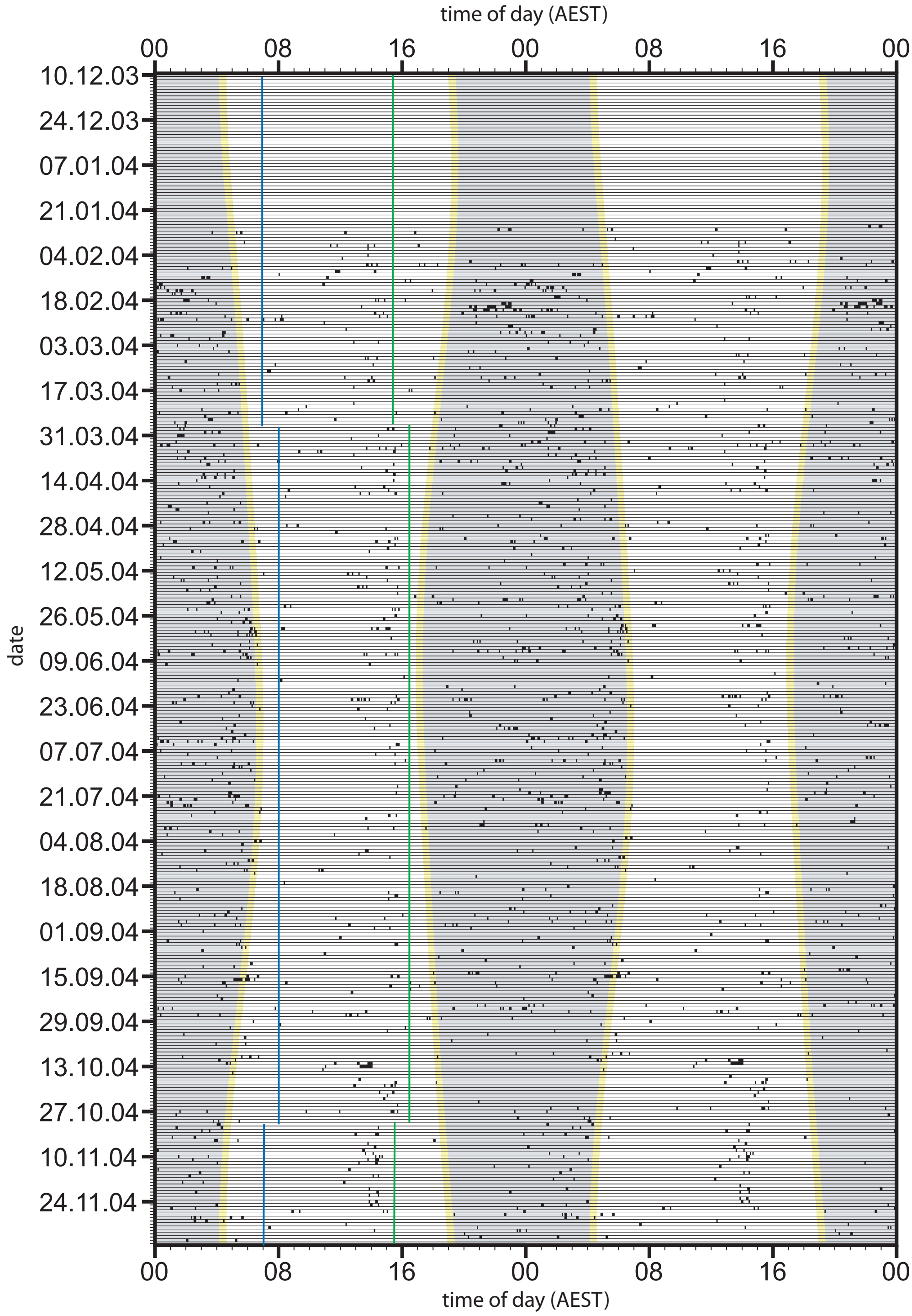

Figure A.14: Presence on ground in the female Carrie for one year.

For further details see A.4.

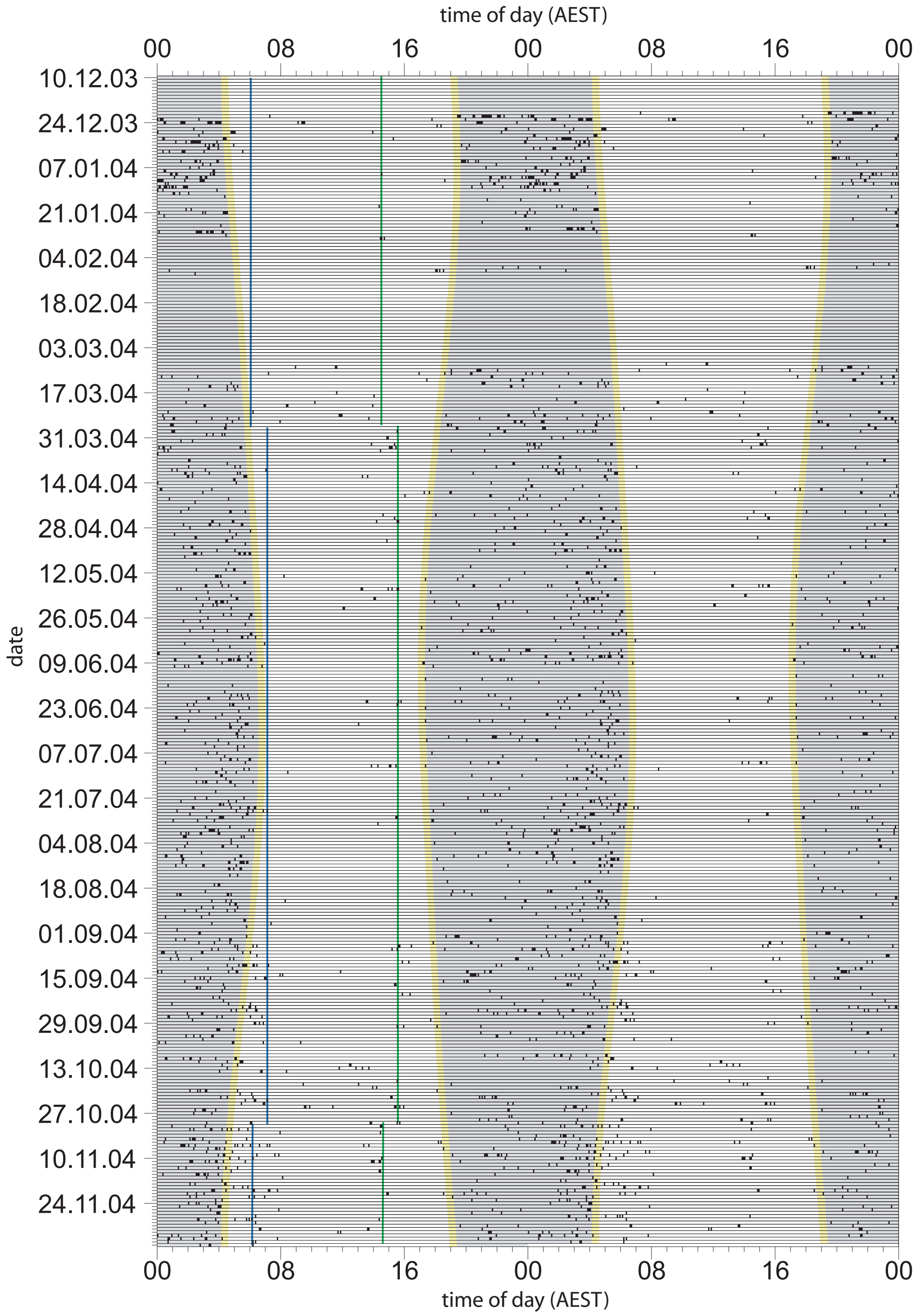

Figure A.15: Presence on ground in the female Yindi for one year.
For further details see A.4.

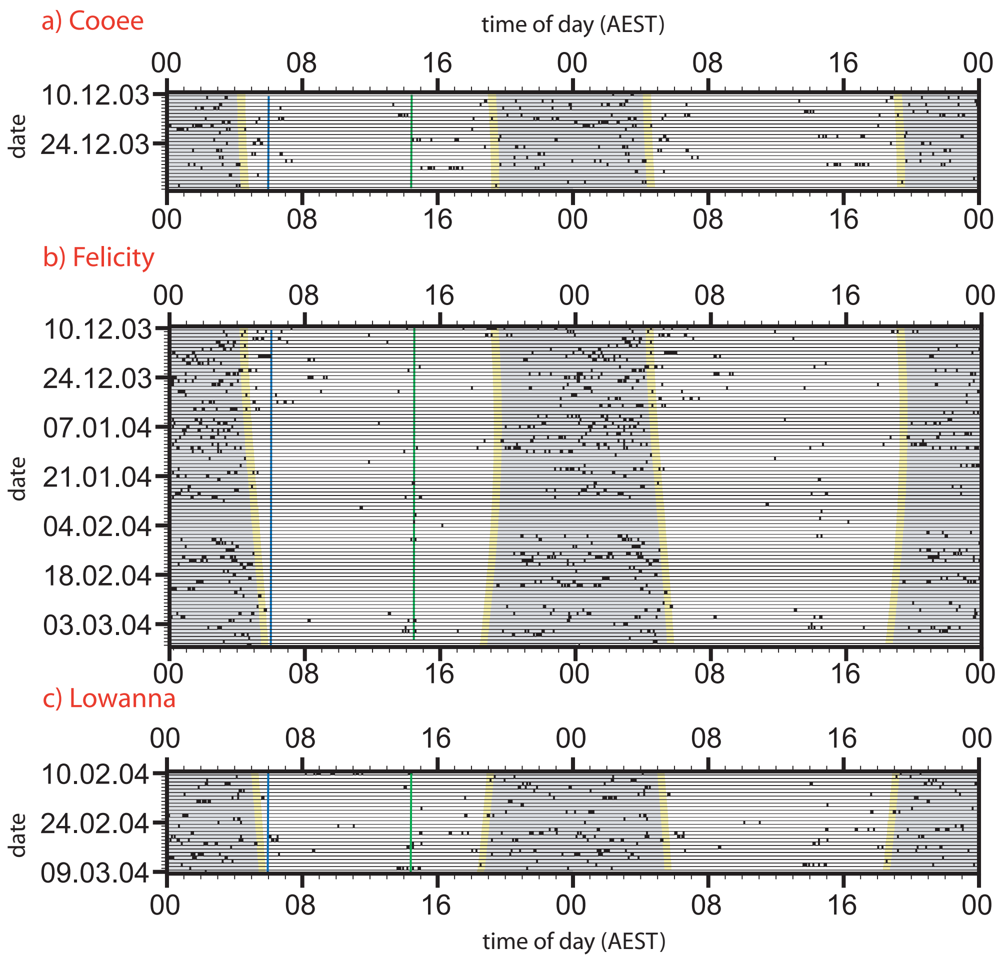

Figure A.16: Presence on the ground in the females Cooee, Felicity and Lowanna during their time at Koala Walkabout.

For further details see A.4.

A.5 Presence in canopy

All figures show double-plotted chronoethograms. Black bars indicate presence in canopy; vertical blue line = morning cleaning, vertical green line= Keeper's Talk. Background colours: grey = night, yellow = twilight.

Fig. A.17: Presence in the canopy in the male Ken for one year.

Ken was rarely observed in the canopy, and if, this usually occurred more often during the day. In winter, he was almost never in the canopy during the day. In spring and in October / November Ken was more often and for a longer time in the canopy at daytime.

Fig. A.18: Presence in the canopy in the female Adori for one year.

Adori was more often in the canopy during the morning, often leaving it at the beginning of the Keeper's Talk. During the remaining afternoon and at night she was less often in the canopy.

Fig. A.19: Presence in the canopy in the female Adori for one year.

Carrie's behaviour showed a clear seasonal change. In summer and spring she was only sometimes seen in the canopy. In winter she spent most of the day there, often leaving the canopy during the Keeper's Talk. At night she was less frequently in the canopy than during daytime.

Fig. A.20: Presence in the canopy in the female Yindi for one year.

Yindi spent most of the day in the canopy, leaving it at dusk. During the night Yindi was less often in the canopy, returning at dawn. In spring she was less often seen in the canopy, but spent still a considerable time there.

Fig. A.21: Presence in the canopy in the females Cooee, Felicity and Lowanna during their time at Koala Walkabout.

The three females spent a considerable part of their day in the canopy, but were rarely there at night. Felicity regularly left the canopy shortly before the Keeper's Talk began.

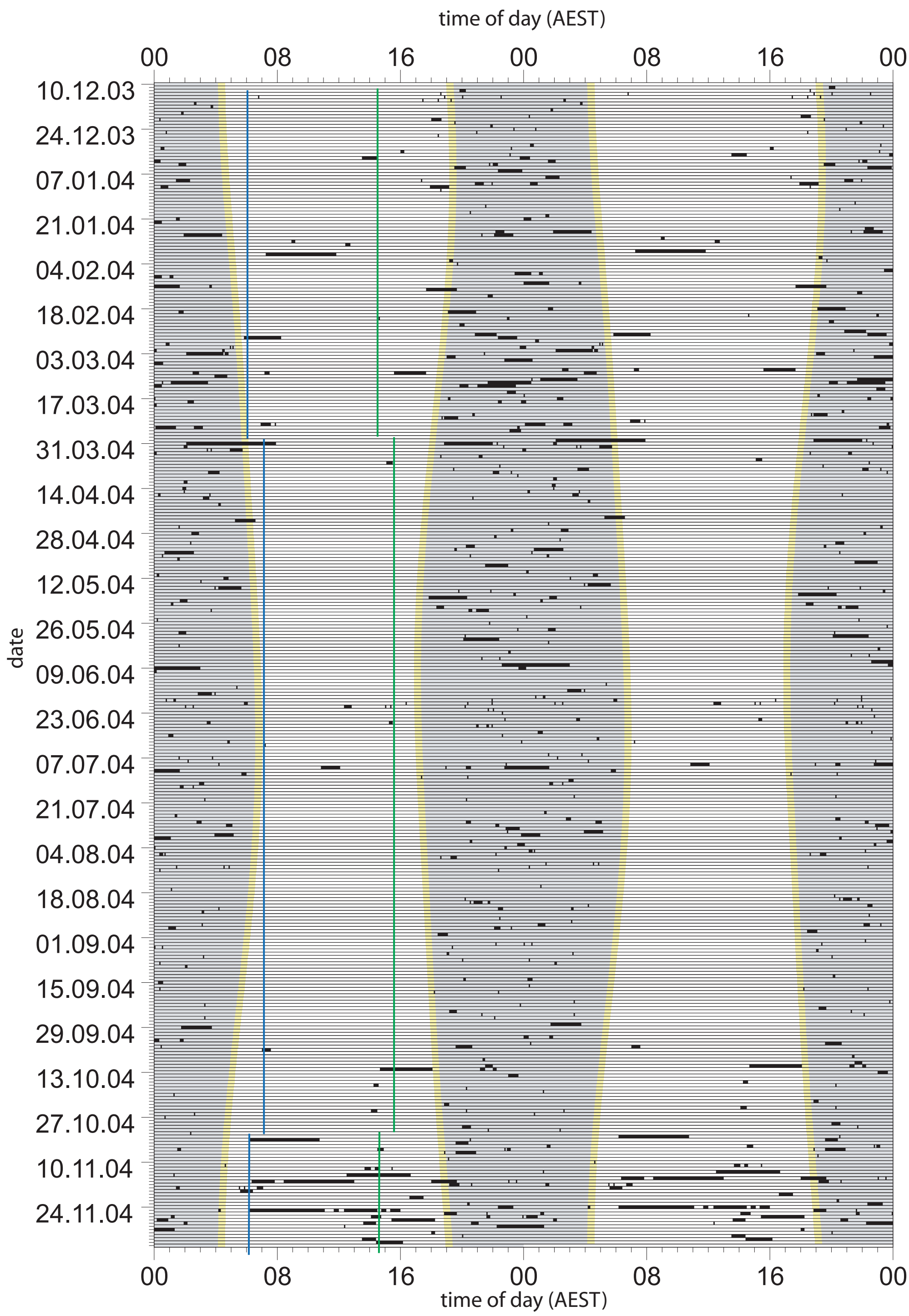

Figure A.17: Presence in the canopy in the male Ken for one year.
For further details see A.5.

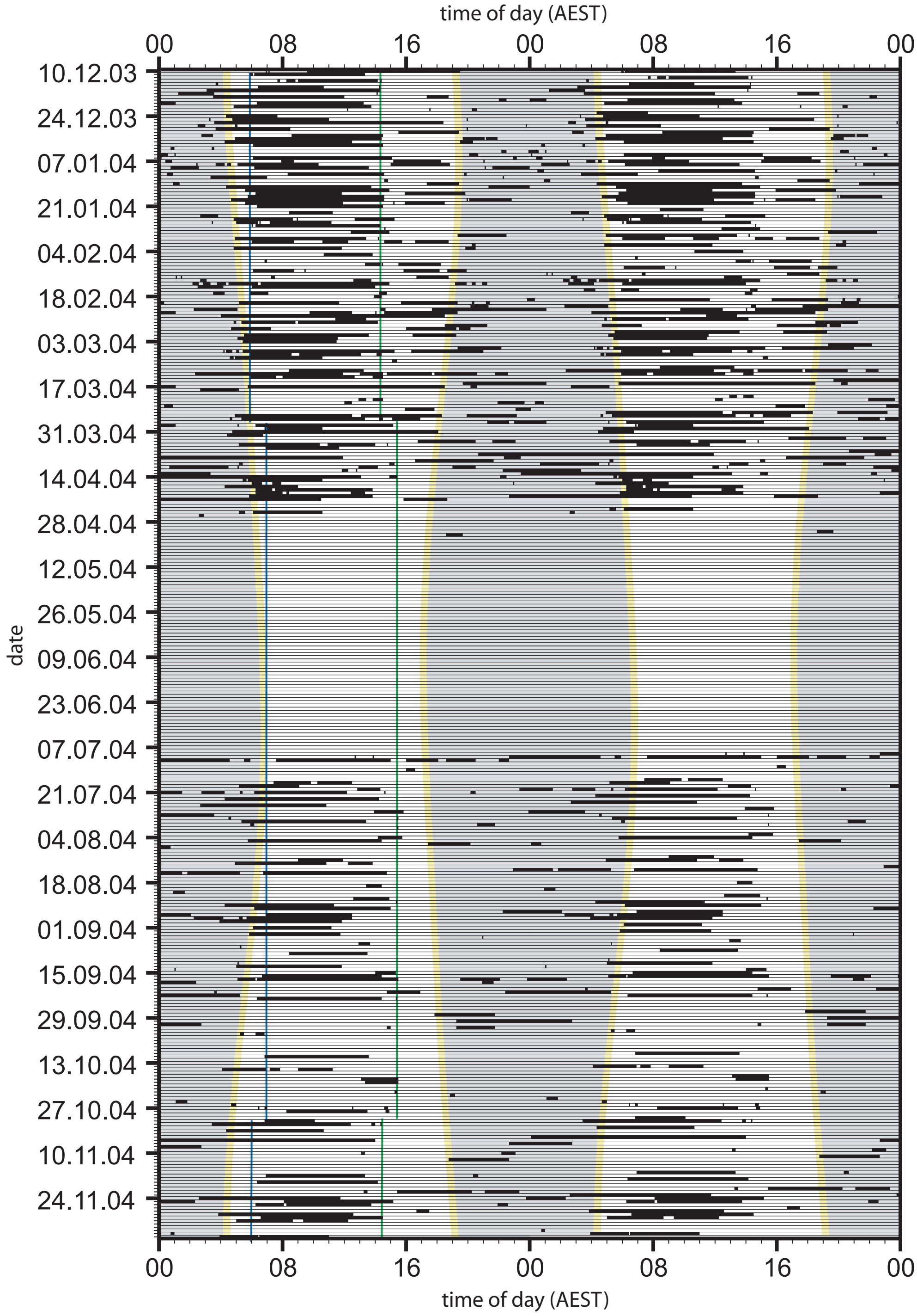

Figure A.18: Presence in the canopy in the female Adori for one year.
For further details see A.5.

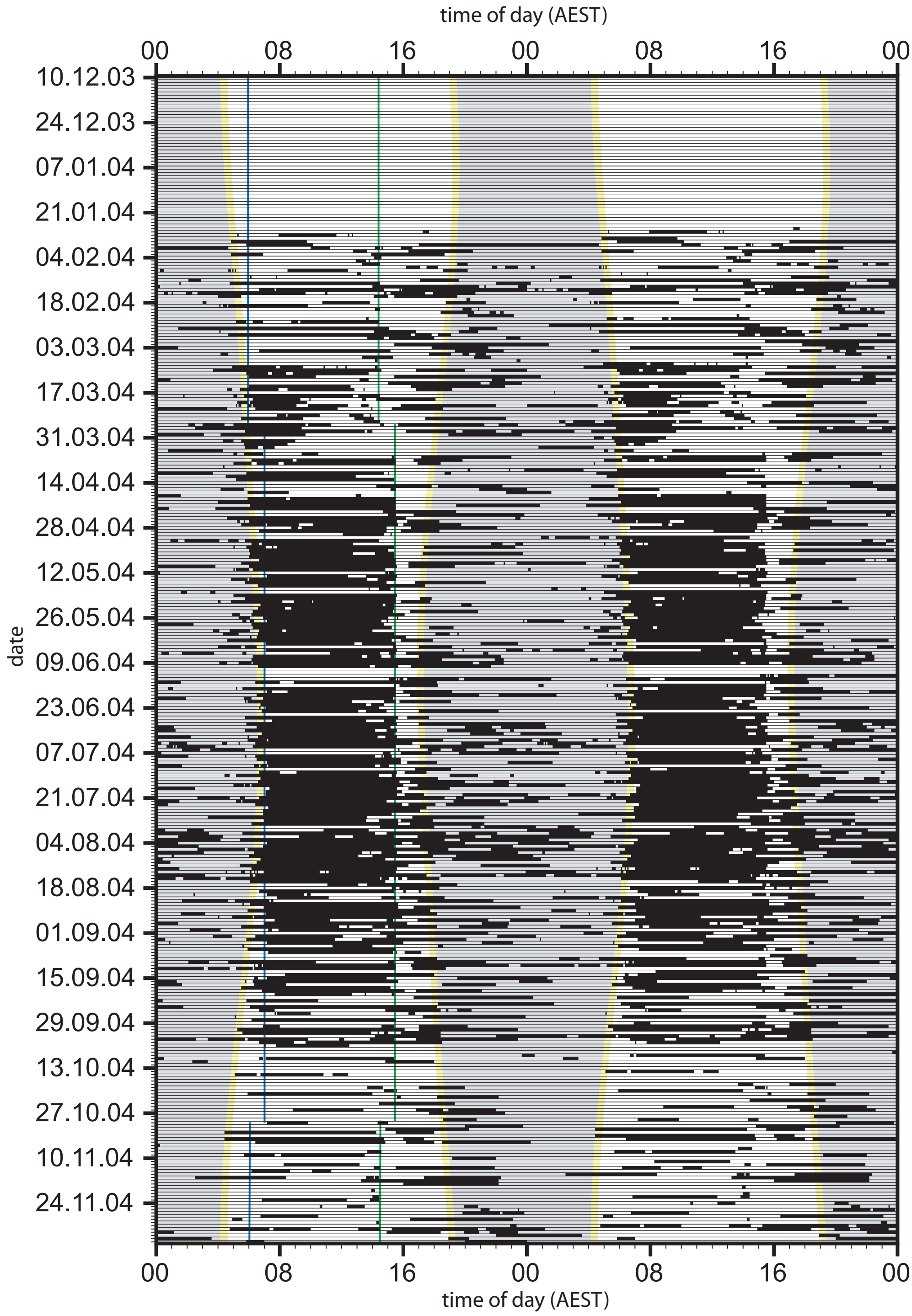

Figure A.19: Presence in the canopy in the female Adori for one year.

For further details see A.5.

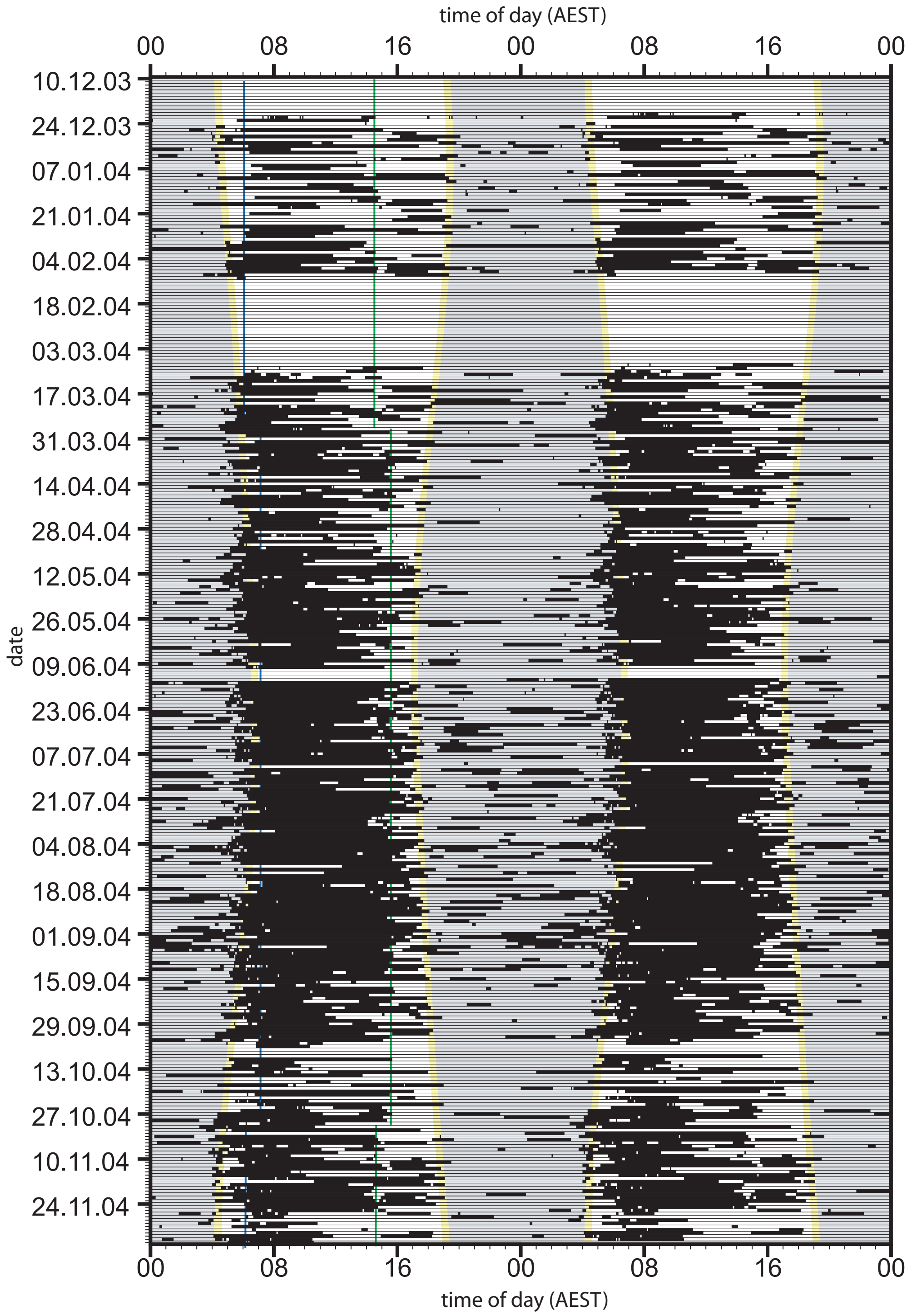

Figure A.20: Presence in the canopy in the female Yindi for one year. For further details see A.5.

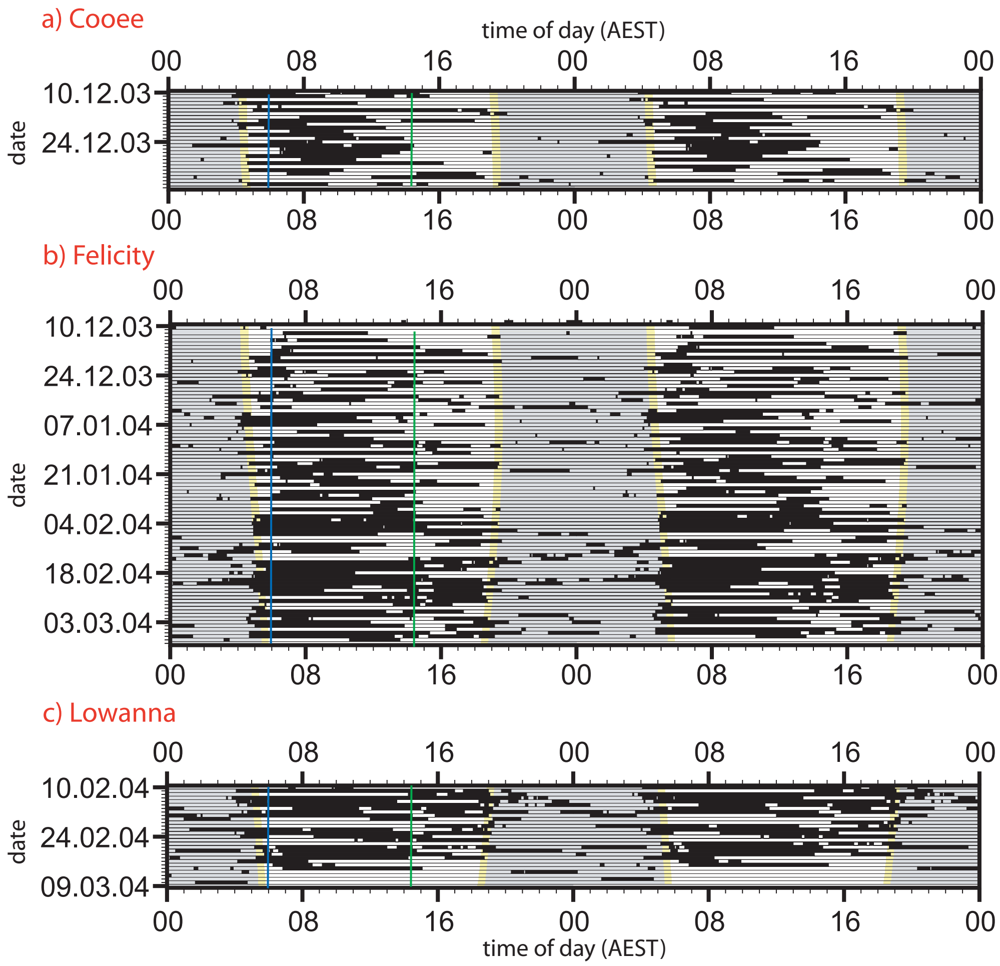

Figure A.21: Presence in the canopy in the females Cooee, Felicity and Lowanna during their time at Koala Walkabout.

For further details see A.5.

A.6 Presence in tree underneath the canopy

All figures show double-plotted chronoethograms. Black bars indicate presence in the tree underneath the canopy; vertical blue line = morning cleaning, vertical green line= Keeper's Talk. Background colours: grey = night, yellow = twilight.

Fig. A.22: Presence in the tree underneath canopy the in the male Ken for one year.

Ken was in the tree rather irregularly and the time spent there varied considerably. Longer periods have usually been observed during the day. Short periods have been observed during the night or prior to the Keeper's Talk.

Fig. A.23: Presence in the tree underneath the canopy the in the female Adori for one year.

Adori was in the tree often prior to the Keeper's Talk. In summer she was rarely seen in the tree during the morning, while in winter there was no difference between night and day.

Fig. A.24: Presence in the tree underneath the canopy in the female Carrie for one year.

Carrie often came to the tree prior to the Keeper's Talk. In summer she spent several hours there during the day, in winter she generally was in the tree less often and was observed there mostly for a short period of time.

Fig. A.25: Presence in the tree underneath the canopy in the female Yindi for one year.

In summer and spring, Yindi was in the tree for longer periods of time, in autumn and winter she was mostly observed there in the afternoon. She frequently was in the tree at night.

Fig. A.26: Presence in the tree underneath the canopy in the females Cooee, Felicity and Lowanna during their time at Koala Walkabout.

The time spent underneath the canopy varied greatly during the time.

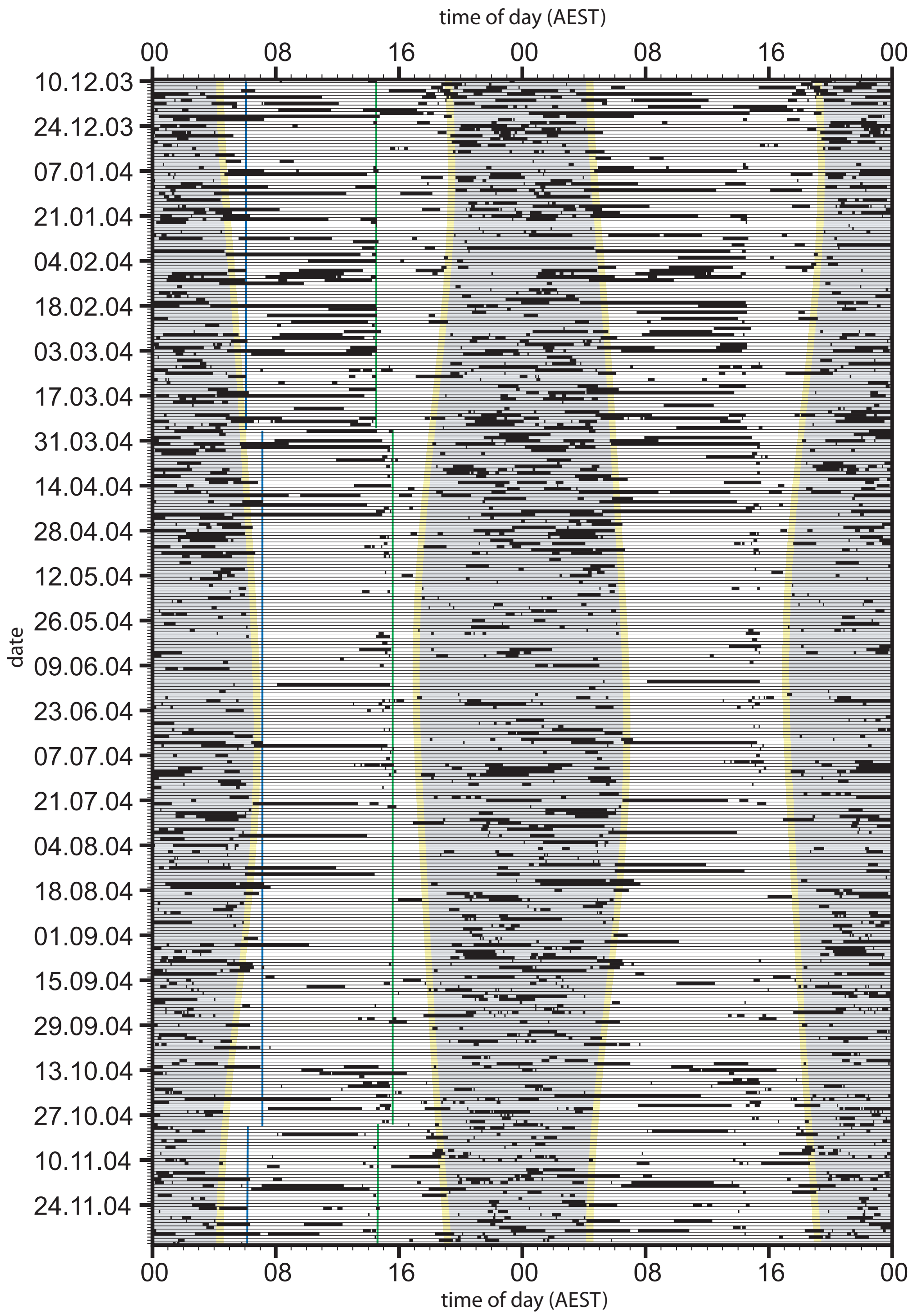

Figure A.22: Presence in the tree underneath canopy the in the male Ken for one year.
For further details see A.6.

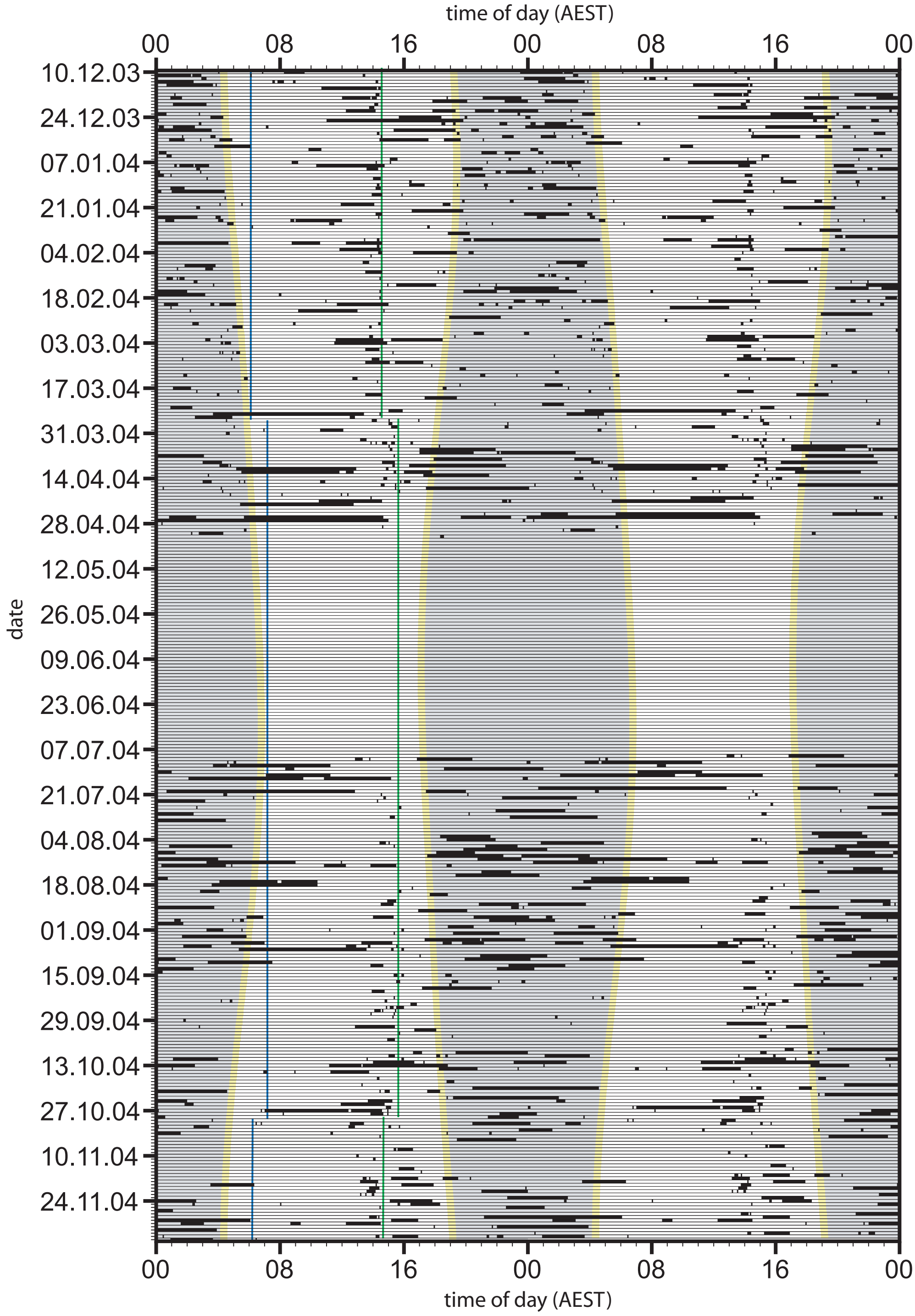

Figure A.23: Presence in the tree underneath the canopy the in the female Adori for one year. For further details see A.6.

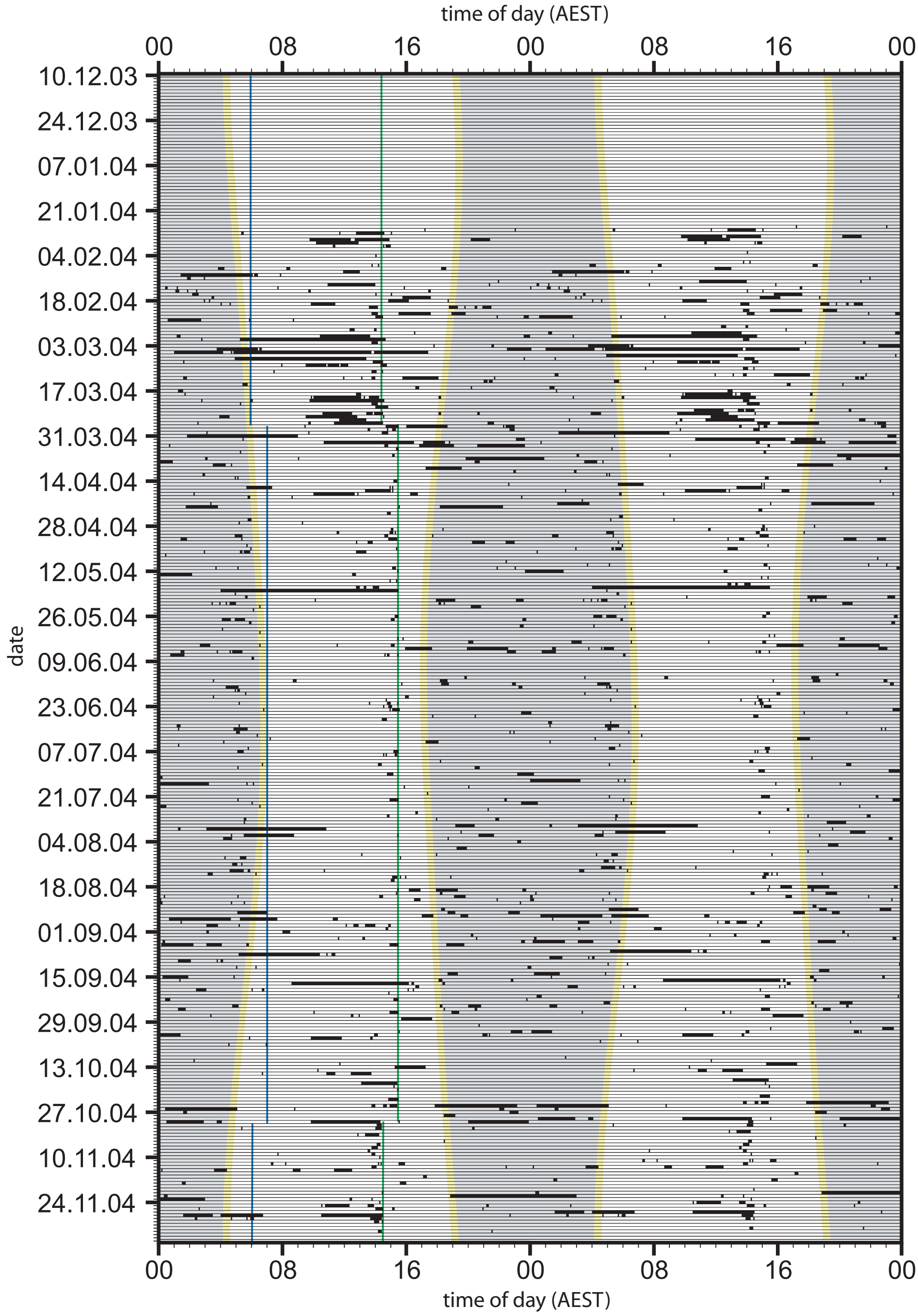

Figure A.24: Presence in the tree underneath the canopy in the female Carrie for one year. For further details see A.6.

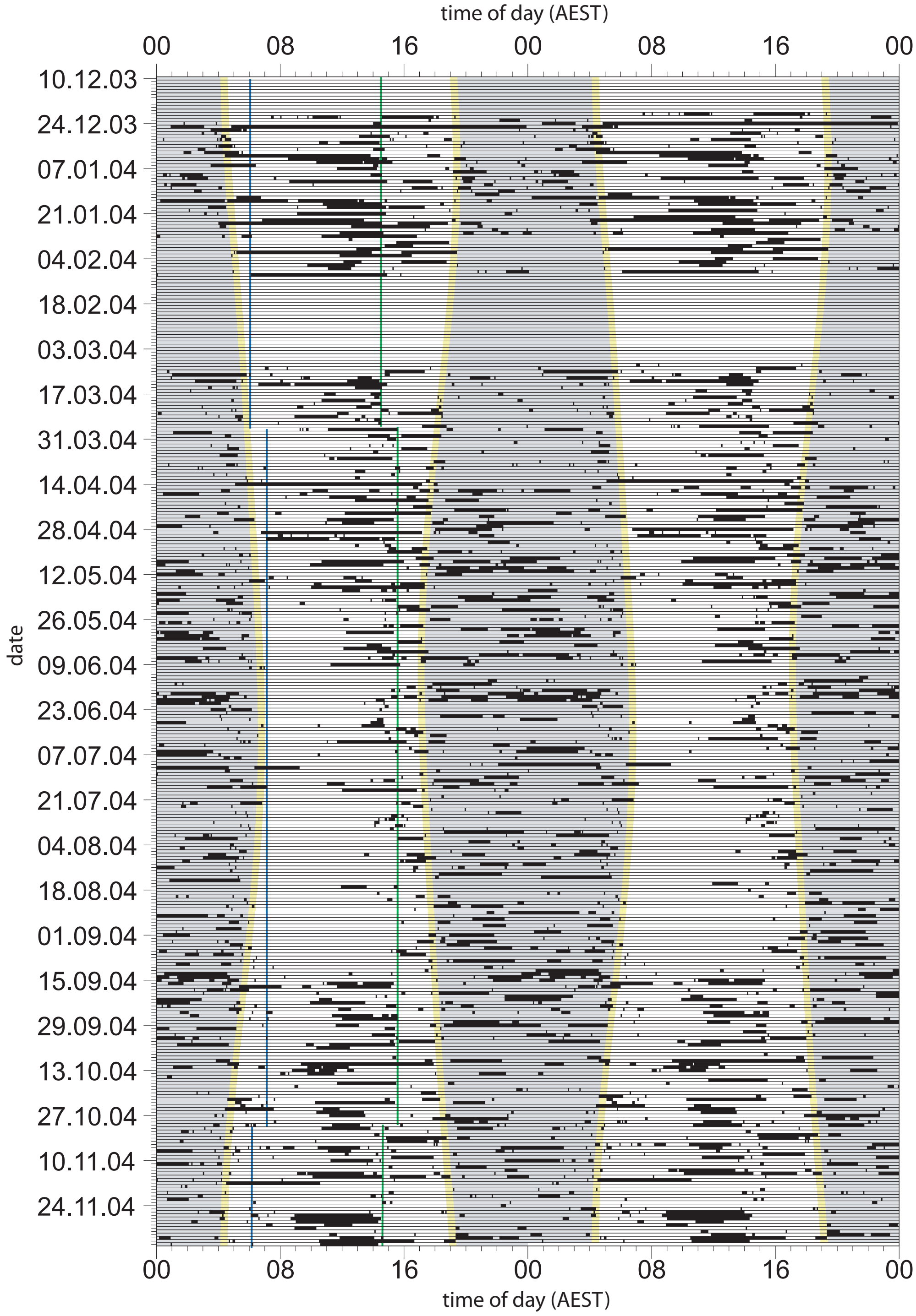

Figure A.25: Presence in the tree underneath the canopy in the female Yindi for one year. For further details see A.6.

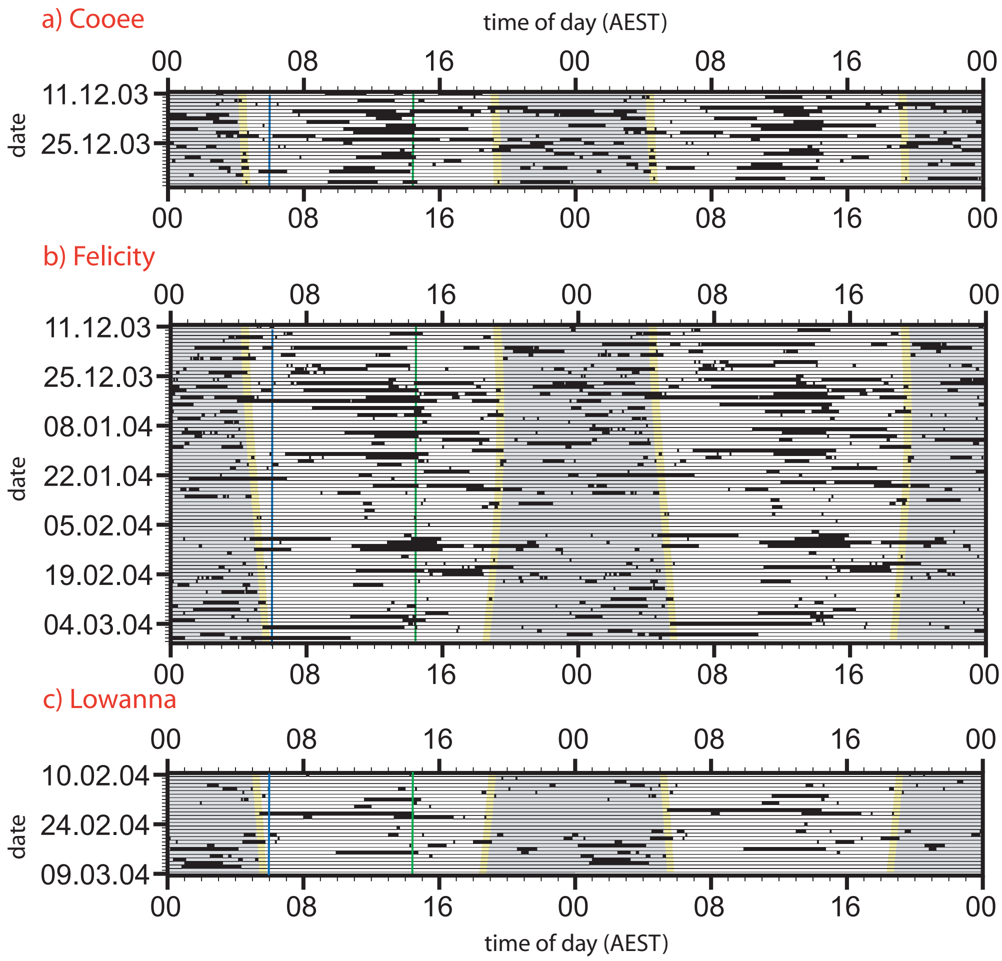

Figure A.26: Presence in the tree underneath the canopy in the females Cooee, Felicity and Lowanna during their time at Koala Walkabout.

For further details see A.6.

Appendix B

Ethograms at Koala Encounter, Taronga Zoo, Sydney

This appendix includes all ethograms of the koalas at Koala Encounter for six weeks of observation, including the yearling Coco.

All figures show double-plotted chronoethograms. Height of columns in actogram indicates level of activity. Blue arrow = morning cleaning session and fresh browse, green arrows = food check and fresh browse if necessary, blue-grey boxes = visitor session.

Fig. B.1: Actograms and activity profiles for total activity in all females at Koala Encounter during six weeks in Southern summer 2004/05.

Females at Bay B showed no clear day/night pattern, while females at Bay C had resting periods during day time. In all koalas there were activity bands at daytime, all related to introduction of new browse or checking of the old browse in the morning and at the beginning of the visitor sessions.

Fig. B.2: Actograms and activity profiles for feeding in all females at Koala Encounter during six weeks in Southern summer 2004/05.

Feeding was displayed with three clear bands in Bay B, which were related to introduction of new browse or checking of the old browse in the morning and at the beginning of the visitor sessions. Levels were low in the mid afternoon, increasing again towards evening with a peak around dusk.

Fig. B.3: Actograms and activity profiles for locomotor activity in all females at Koala Encounter during six weeks in Southern summer 2004/05.

Locomotor activity was more common during the night and in the morning, particularly in Cooee and Coco. In all koalas locomotor activity was higher at certain times of observation. In most cases this corresponded with another koala in the enclosure.

Fig. B.4: Actograms and activity profiles for presence on ground in all females at Koala Encounter during six weeks in Southern summer 2004/05.

All koalas have been observed more often on the ground during the night. In Bay B the females have been longer on the ground in the first week. Cooee and Coco were very often on the ground in week 5, when locomotion activity was high too (see Fig. B.3).

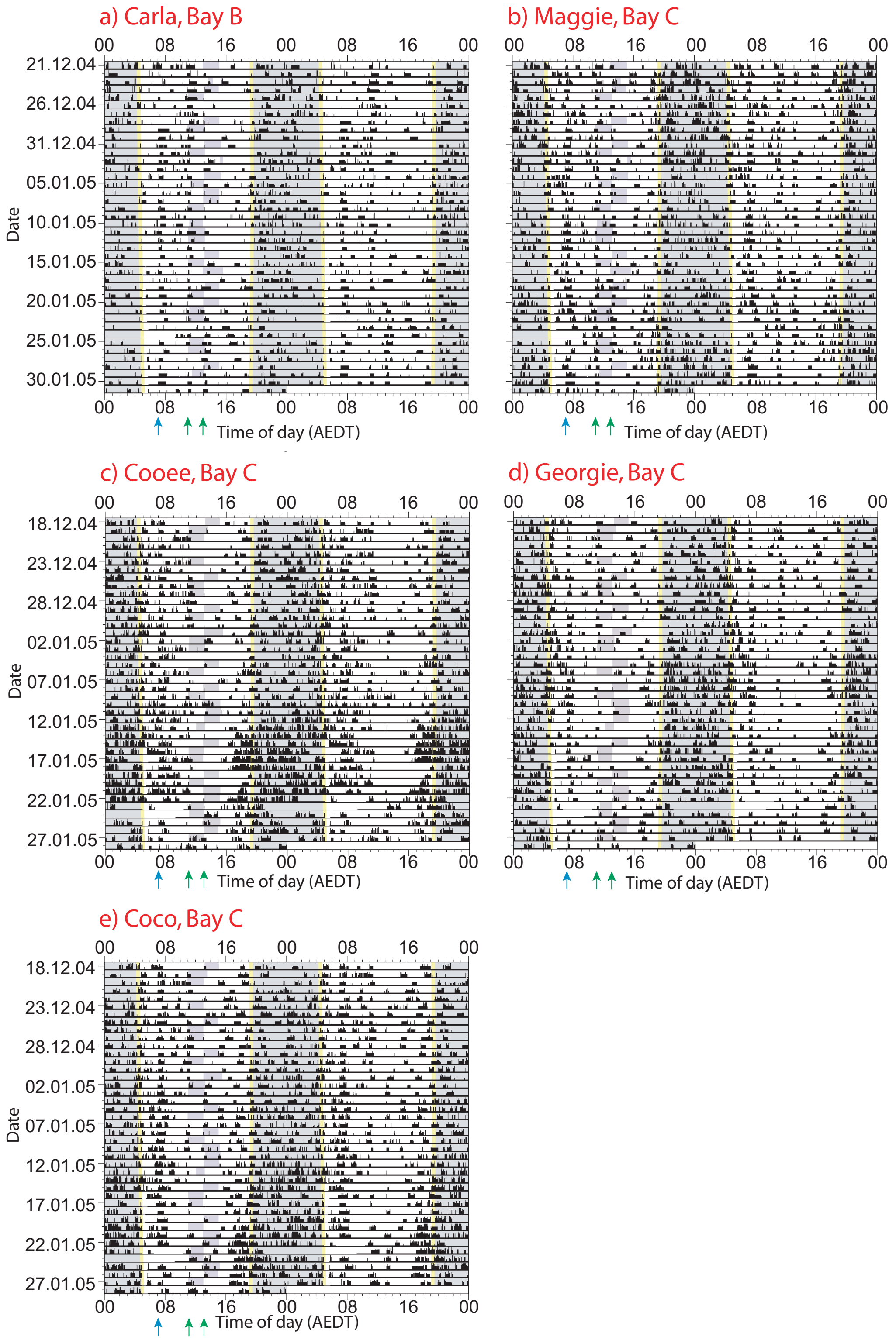

Figure B.1: Actograms and activity profiles for total activity in all females at Koala Encounter during six weeks in Southern summer 2004/05.

For further details see B.

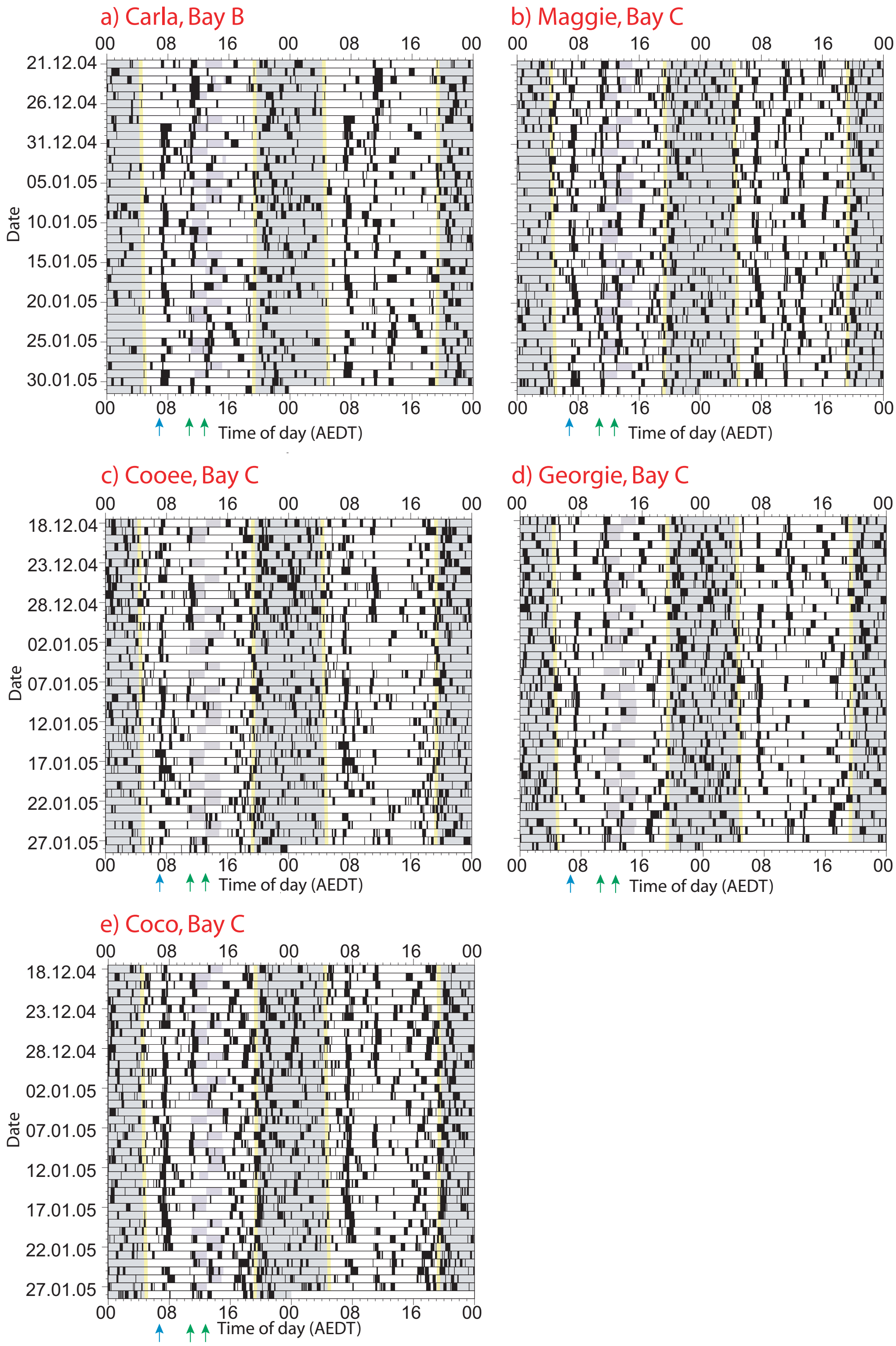

Figure B.2: Actograms and activity profiles for feeding in all females at Koala Encounter during six weeks in Southern summer 2004/05.

For further details see B.

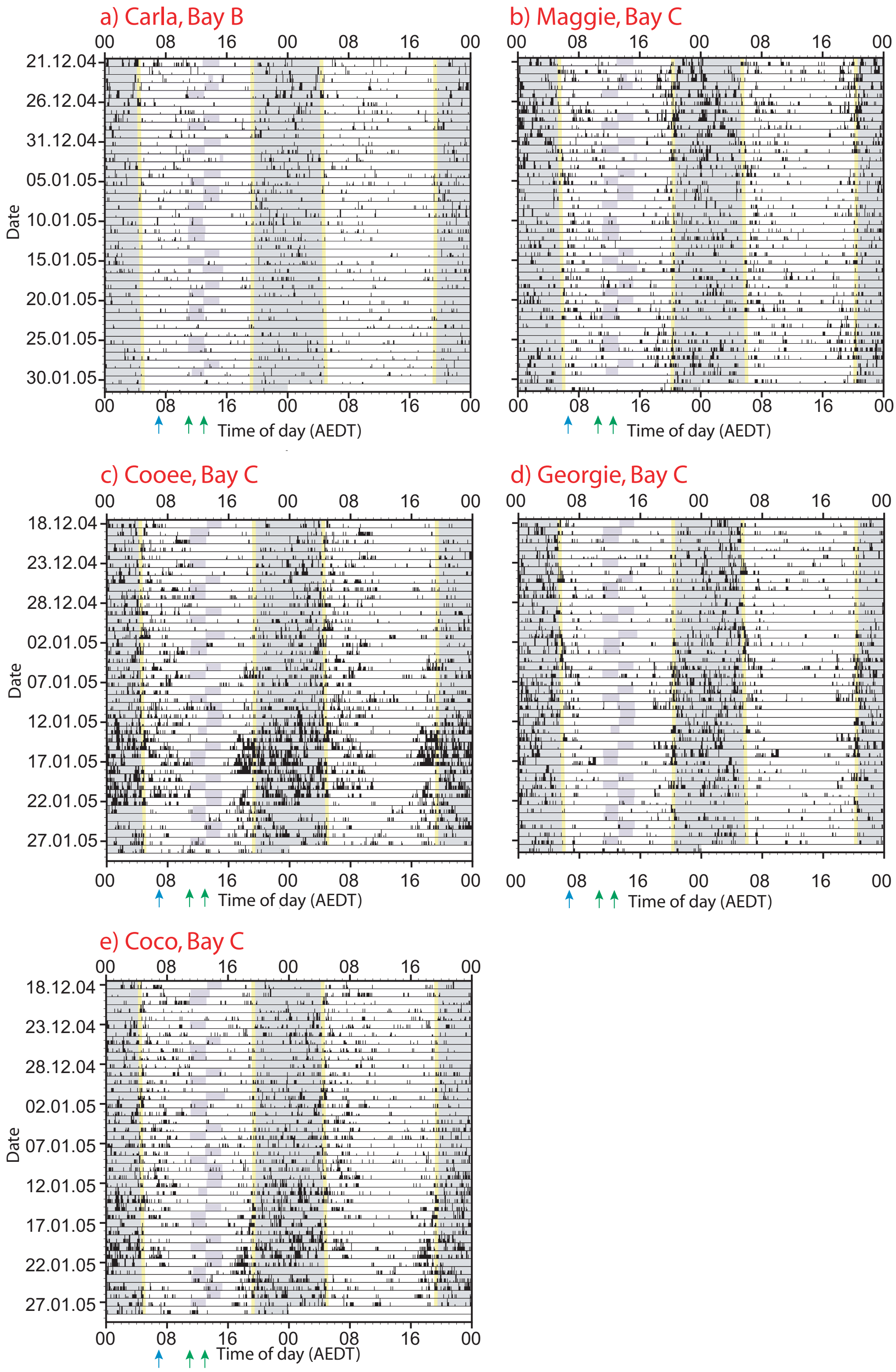

Figure B.3: Actograms and activity profiles for locomotor activity in all females at Koala Encounter during six weeks in Southern summer 2004/05.

For legend see B.

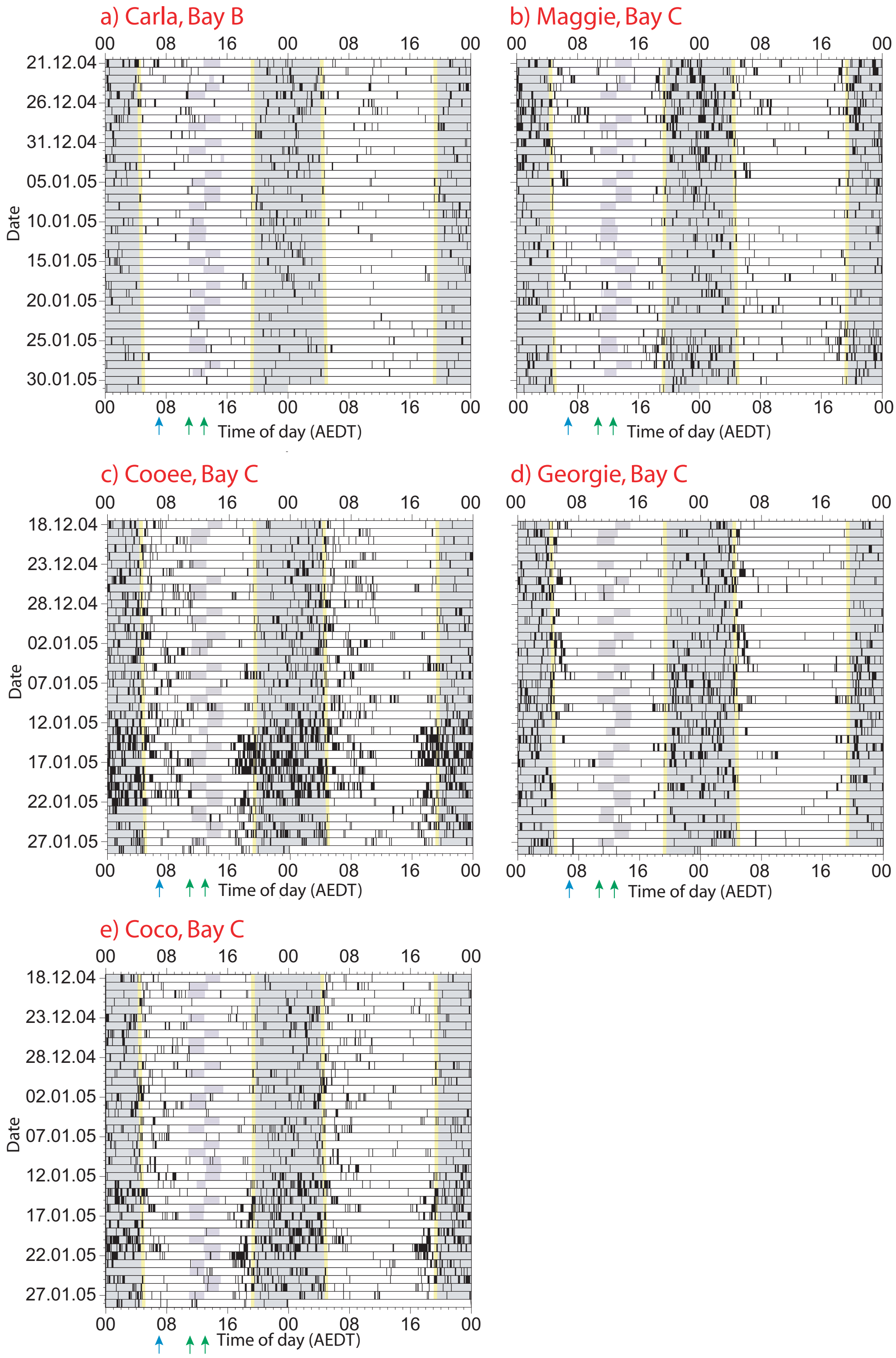

Figure B.4: Actograms and activity profiles for presence on ground in all females at Koala Encounter during six weeks in Southern summer 2004/05.

For legend see B.

Appendix C

Individual time budgets and day:night ratios for all observed koalas

Diagrams show individual time budgets as percentage of 5 min observation intervals per 24 hours or day:night ratio. If not indicated otherwise, data are calculated from 42 days of observation. The bars indicate the standard deviation between single days.

Koalas in Sydney and Duisburg have been tested for significant differences with Univariate Repeated-Measurement ANOVA and Tuckey Posthoc-test (Resting, Feeding and Loc2) or Friedman ANOVA (Loc1, Loc3 and Presence on ground). Koalas in Vienna have been compared with t-test (Resting, Feeding, Loc2) and Kolmogorov-Smirnoff-Z-Test (Loc1, Loc3 and Presence on ground). Significant differences between koalas are either indicated by asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) or by letters.

Feeding and Loc2 have been regularly observed in one interval. In this case, the interval was counted for both behaviours, so the sum of all behaviour is bigger than 100%. Presence on ground is counted independently.

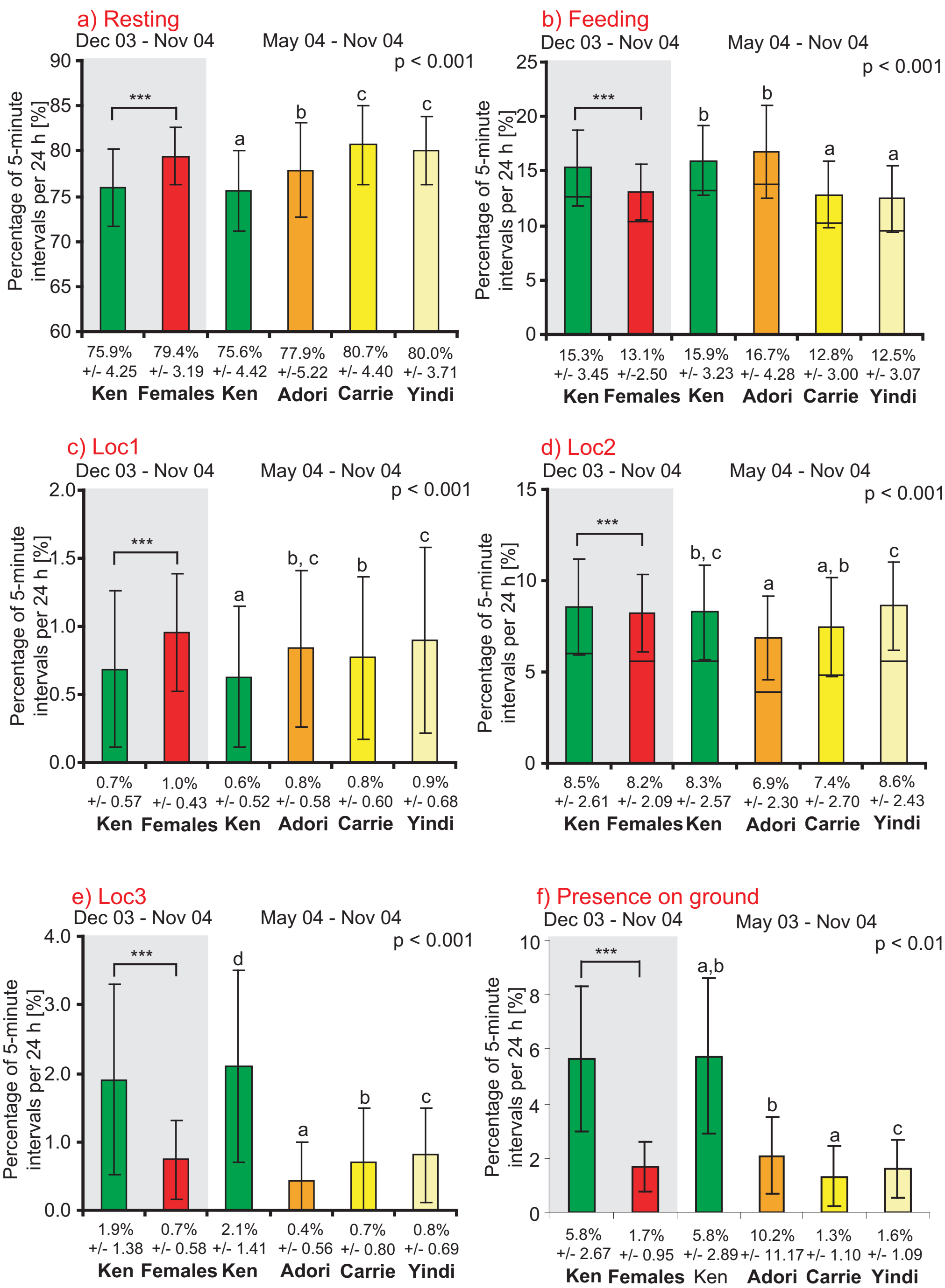

Figure C.1: Individual time budgets for all behaviour categories at Koala Walkabout, Sydney.

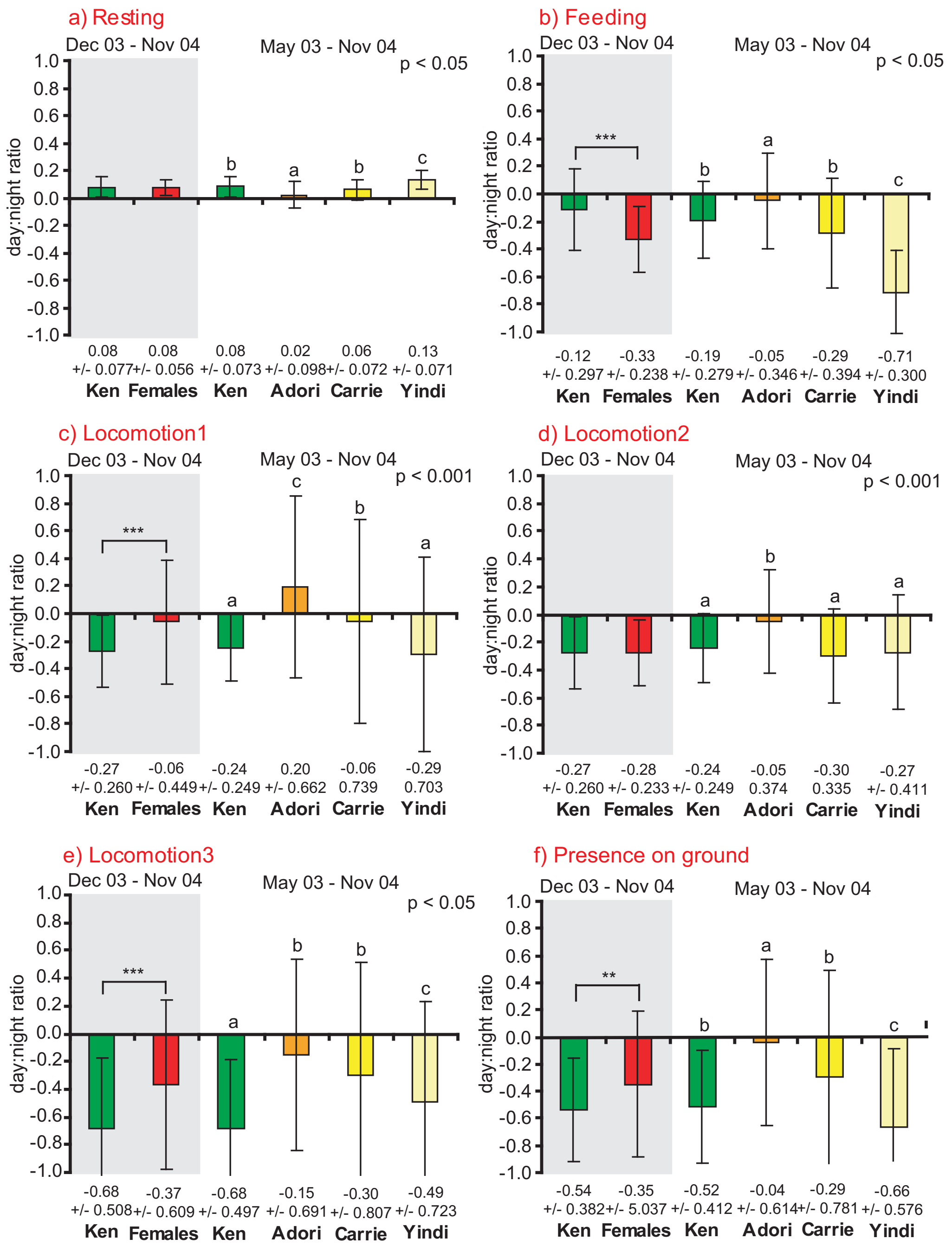

Figure C.2: Individual day:night ratios for all behaviour categories at Koala Walkabout, Sydney.

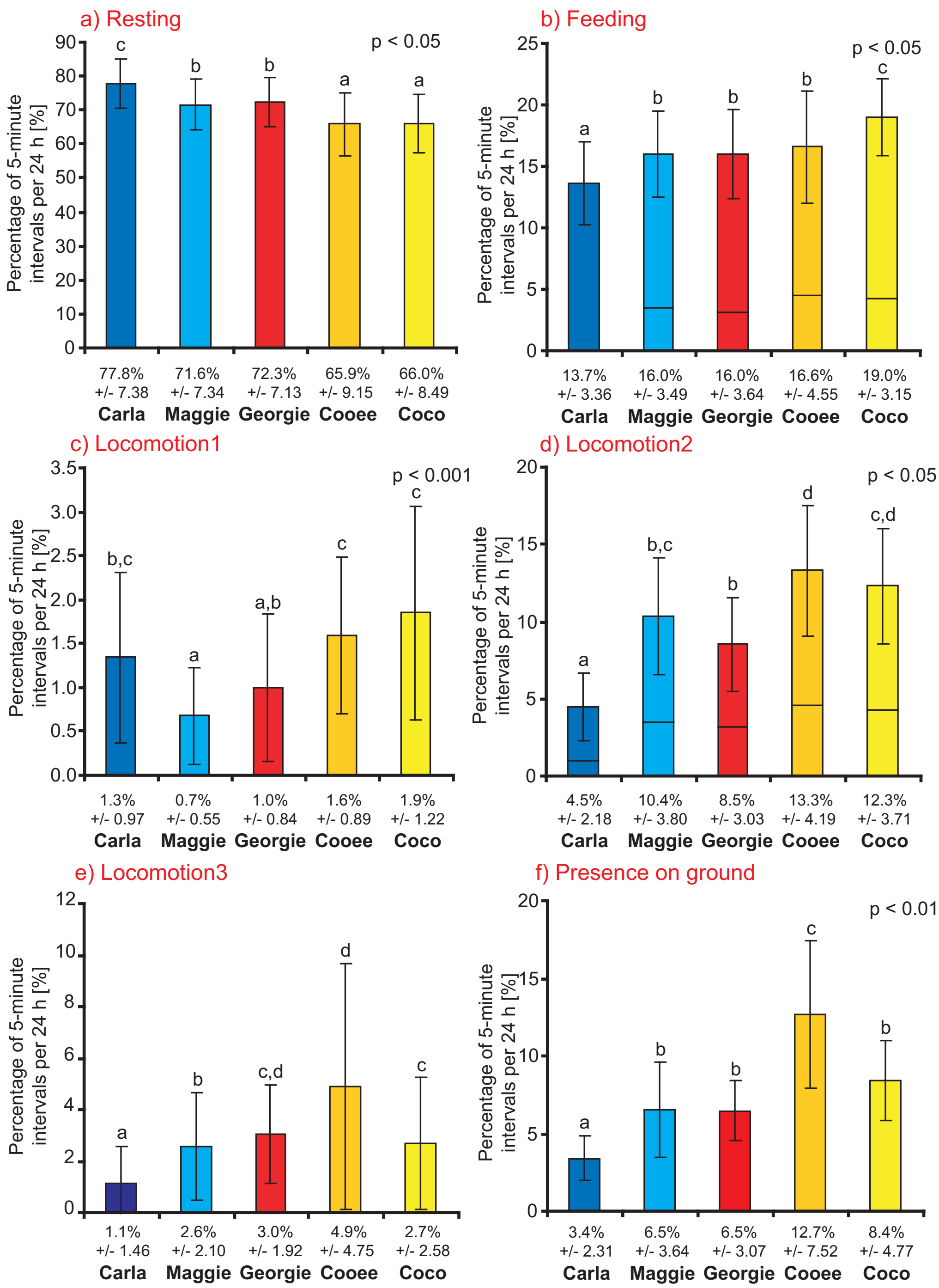

Figure C.3: Individual time budgets for all behaviour categories at Koala Encounter, Sydney.

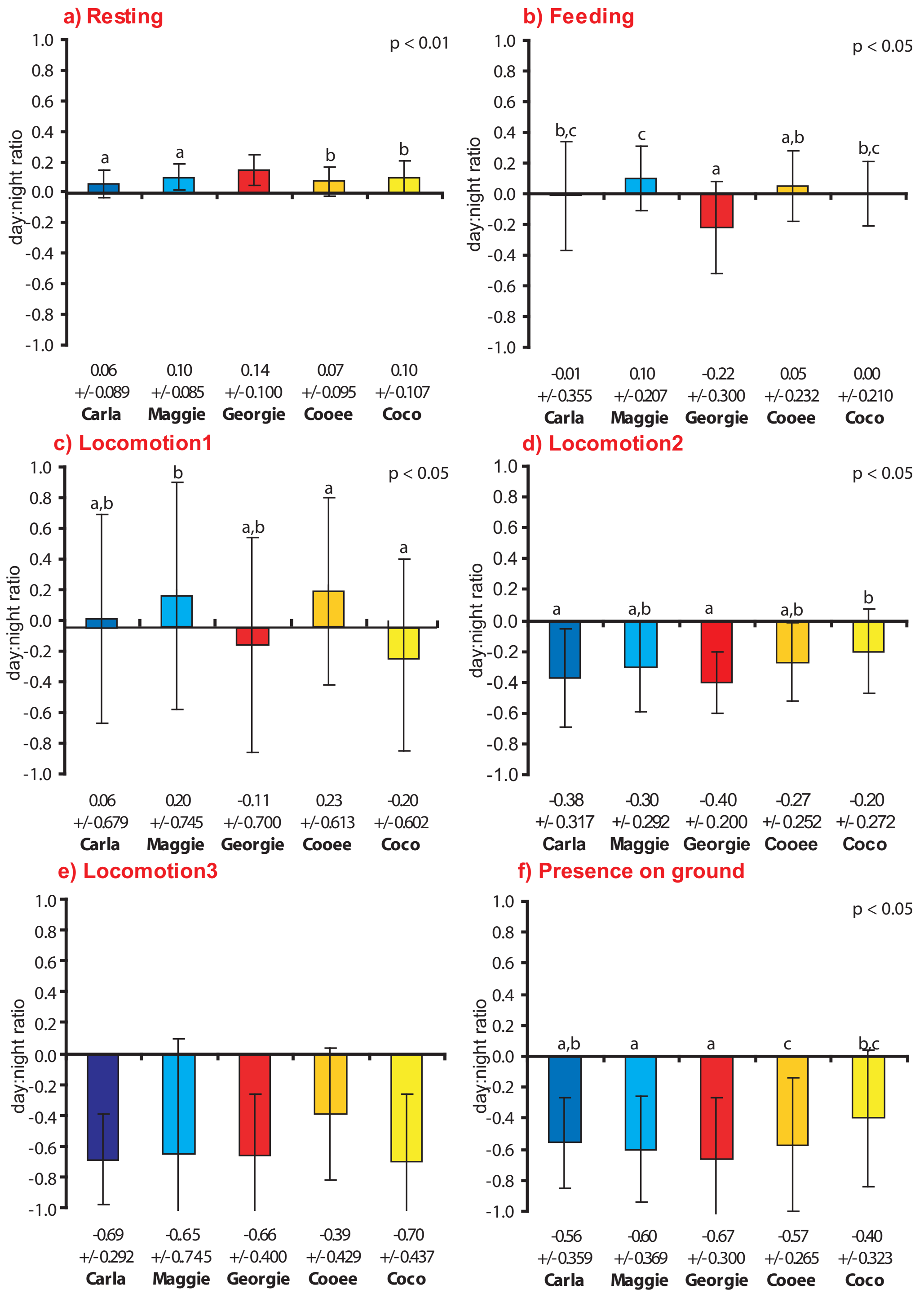

Figure C.4: Individual day:night ratios for all behaviour categories at Koala Encounter, Sydney.

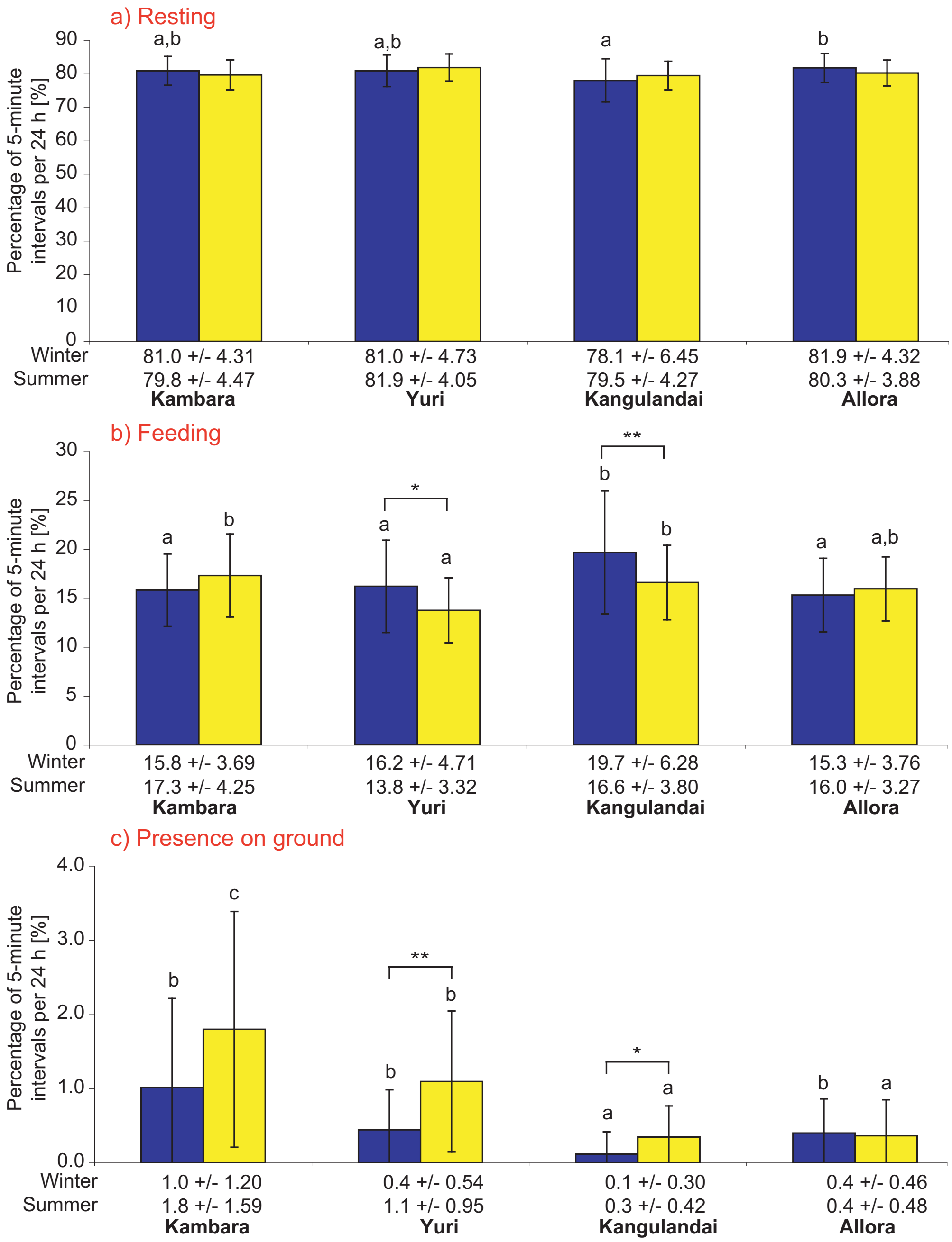

Figure C.5: Individual time budgets for resting, feeding and presence on ground at Duisburg Zoo.

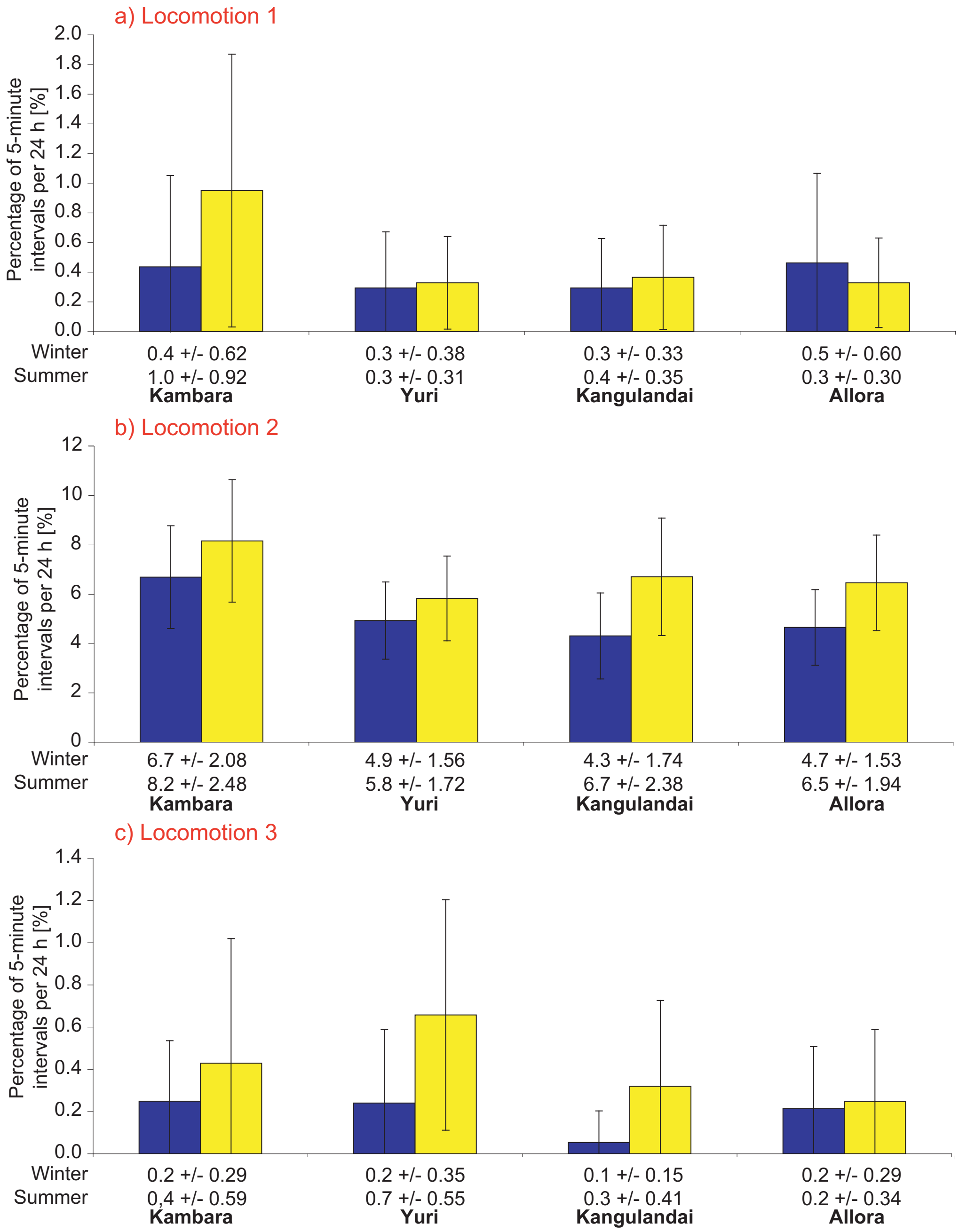

Figure C.6: Individual time budgets for locomotor activity at Duisburg Zoo.

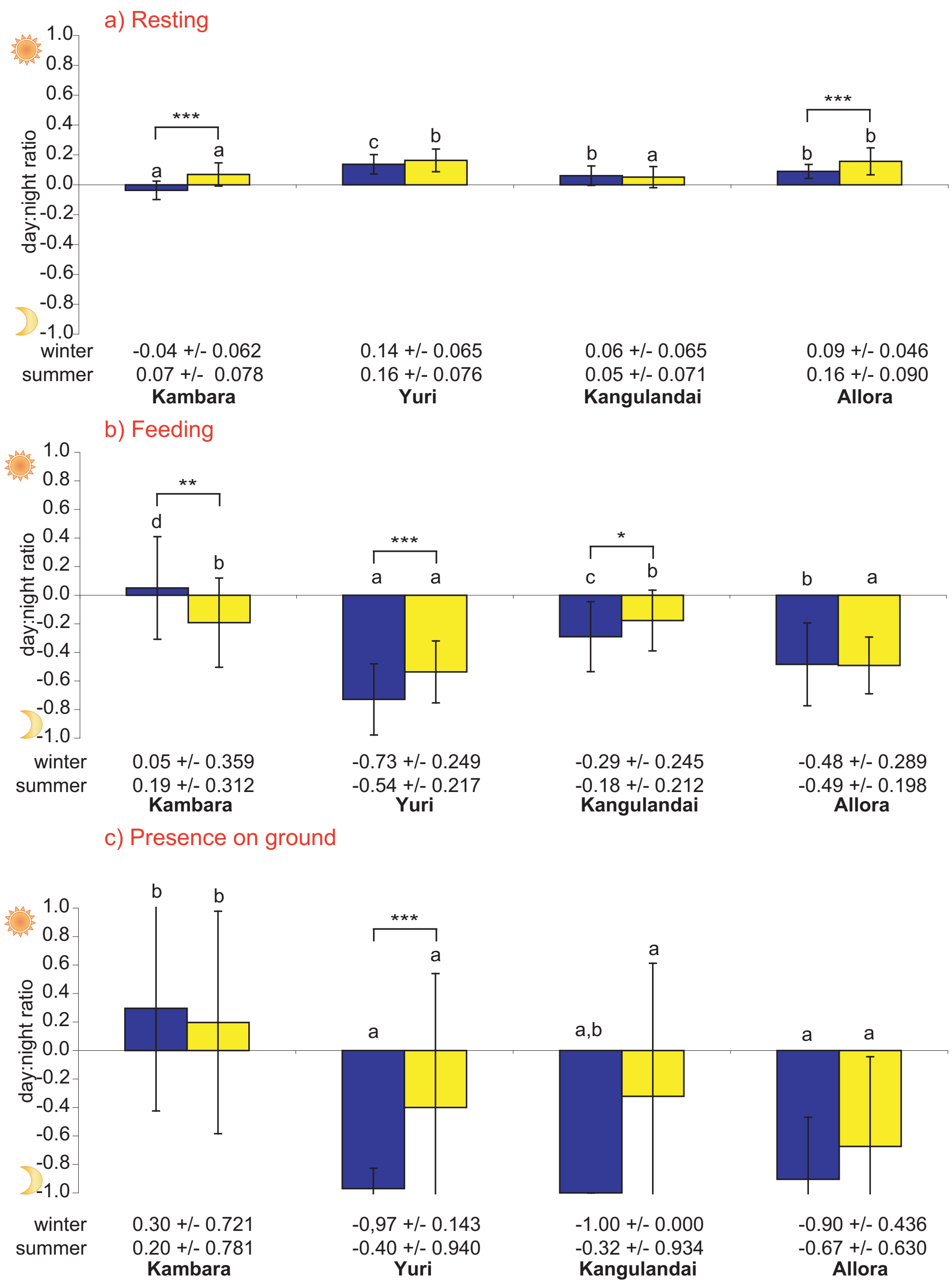

Figure C.7: Individual day:night ratios for resting, feeding and presence on ground at Duisburg Zoo.

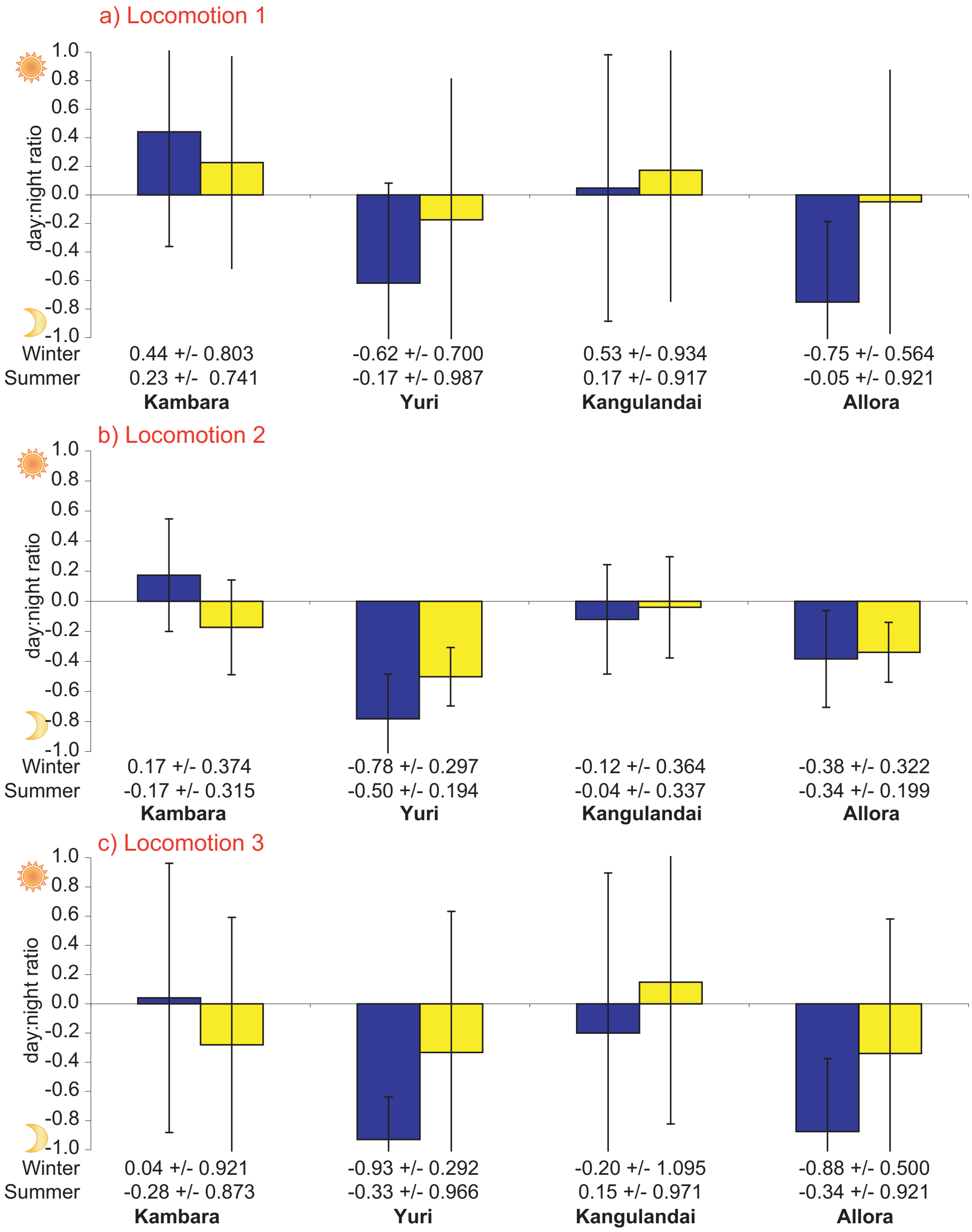

Figure C.8: Individual day:night ratios for locomotor activity at Duisburg Zoo.

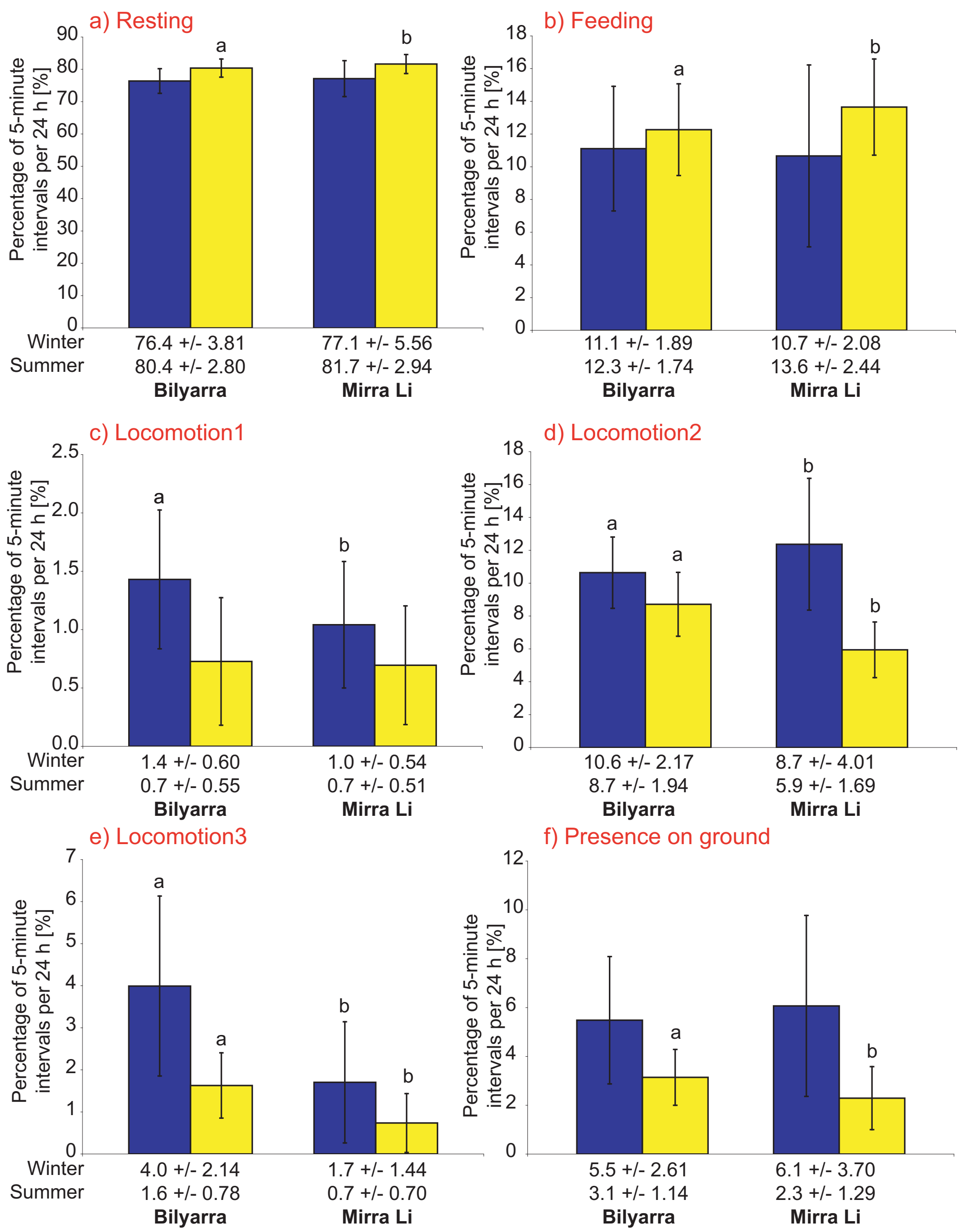

Figure C.9: Individual time budgets for all behaviour categories at Vienna Zoo.

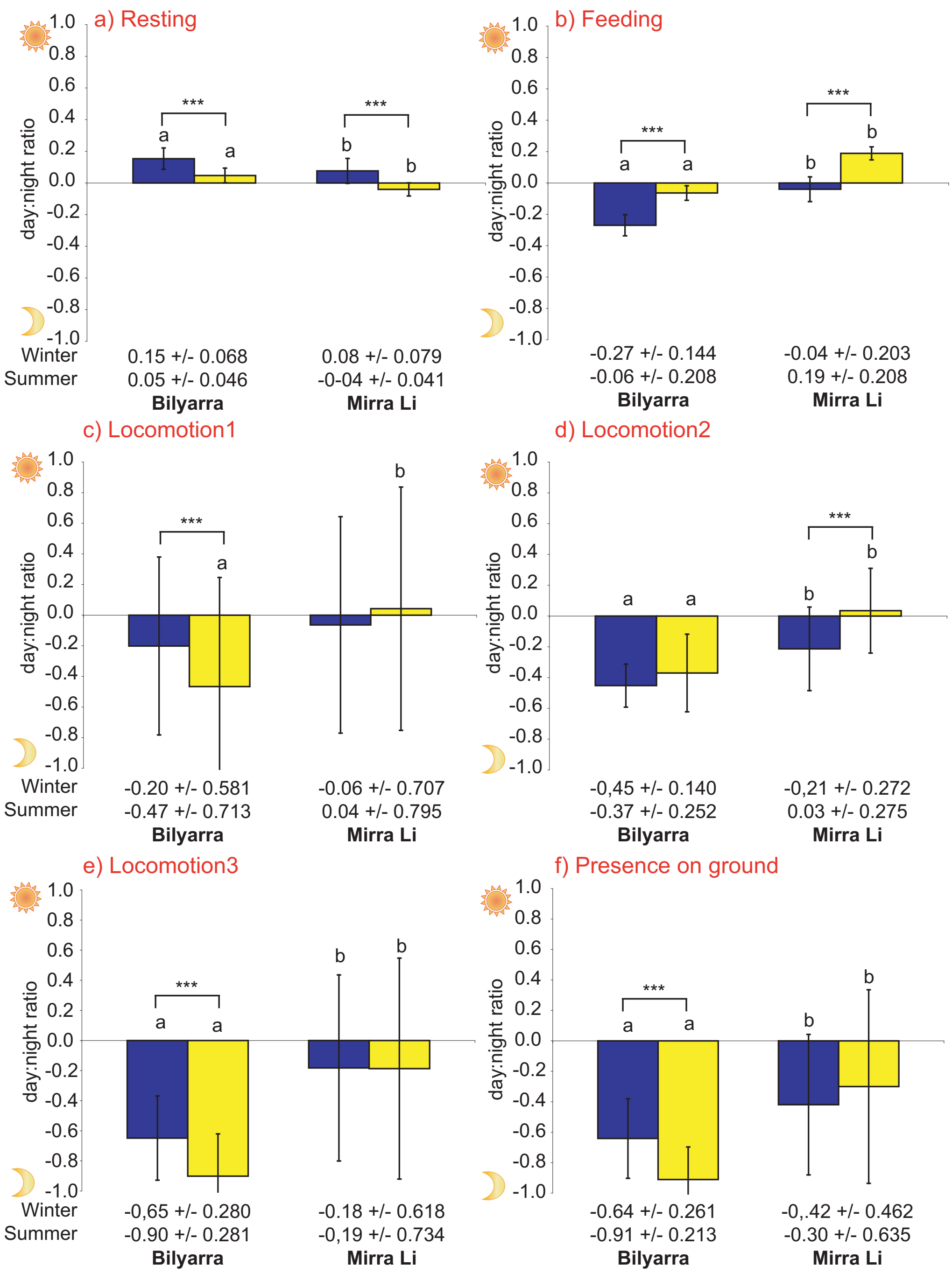

Figure C.10: Individual day:night ratios for all behaviour categories at Vienna Zoo.

Appendix D

Meteorological data for Sydney

Sydney lies within the temperate zone of Australia. Since it is on the Southern hemisphere, seasons are reversed. The weather is usually without extremes in heat or cold. The summers are warm and humid with frequent thunderstorms. Different to the Blue Mountains about 200 km away there is no snow in winter. Temperatures are mild. Winter is the usual rain season, but this was not the case in 2004. Beginning in 2003, rainfall had been reduced considerably and water restriction were installed in Sydney in summer 2003/04.

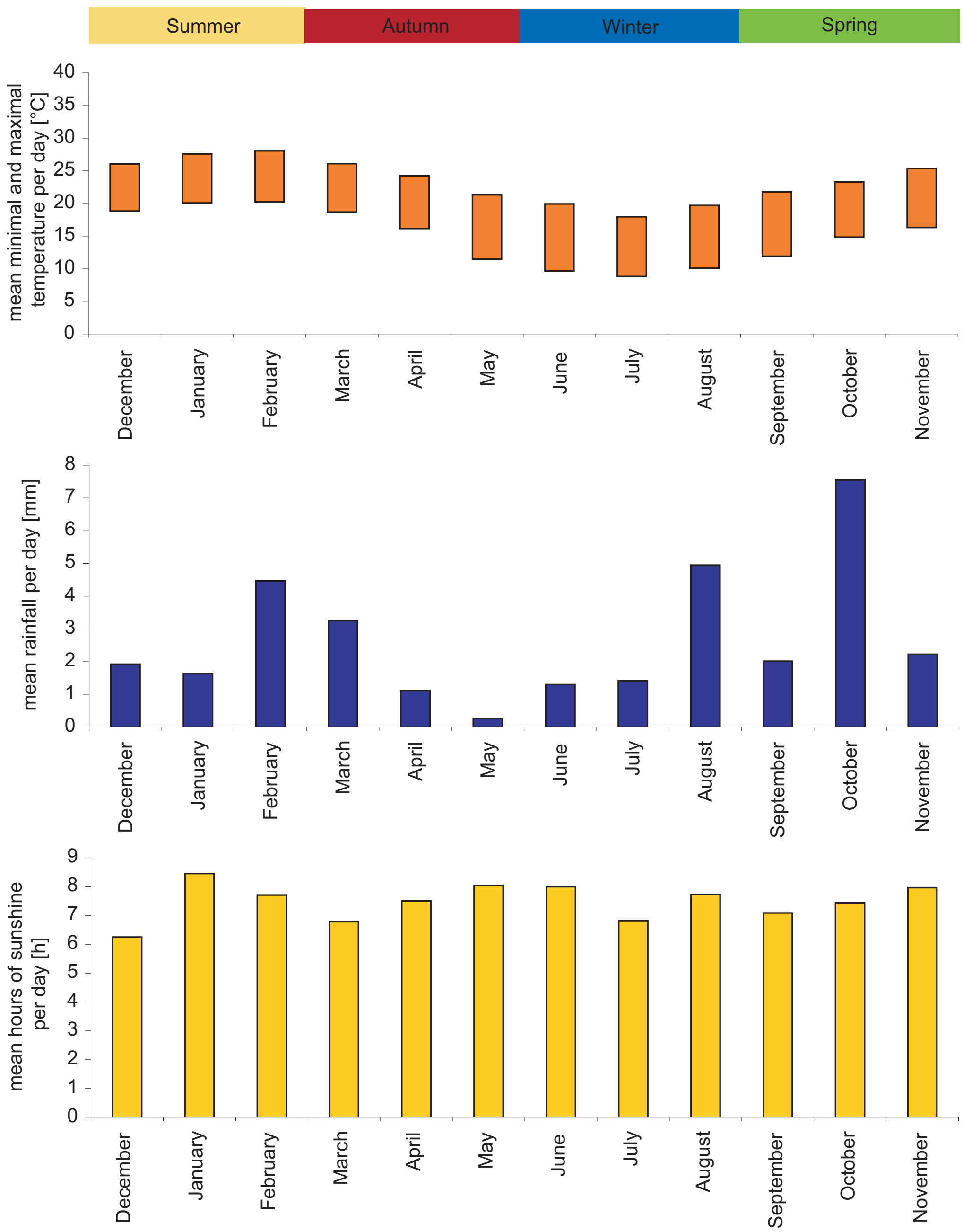

Figure D.1: Mean daily temperature minima and maxima, mean daily rainfall and mean hours of sunshine per day for Sydney between 1 December 2003 and 30 November 2004. Data were obtained from Commonwealth Bureau of Meteorology. Temperature and humidity were measured at Observatory Hill (station 066062), hours of sunshine at Sydney Airport (station 066037).

Appendix E

Times of photo sessions at Koala Encounter

	Bay B		Bay C	
Date	Begin	End	Begin	End
18. Dec	11:00	13:00	13:10	15:00
19. Dec			11:00	13:25
20. Dec			10:50	13:00
21. Dec	12:55	15:30	10:55	12:55
22. Dec				
23. Dec	15:20	15:30	10:55	12:55
24. Dec	13:10	14:50		
25. Dec	10:55	12:55	13:10	14:50
26. Dec			10:55	12:55
27. Dec			11:05	12:55
28. Dec	13:00	14:55		
29. Dec	10:55	13:00	13:00	15:00
30. Dec			10:55	12:55
31. Dec	13:05	15:05		
01. Jan	11:00	13:00	13:00	15:25
02. Jan	15:10	15:25	11:05	13:10
03. Jan			11:00	13:05

continued on next page

continued from last page

	Bay B		Bay C	
Date	Begin	End	Begin	End
04. Jan	13:05	15:05		
05. Jan	11:15	12:55	13:00	14:55
06. Jan	13:00	15:00	10:55	12:55
07. Jan	13:00	14:55		
08. Jan	11:00	12:55	13:00	14:55
09. Jan			10:55	13:00
10. Jan	11:10	12:45	12:50	15:05
11. Jan	11:00	13:10	13:15	15:10
12. Jan	11:00	13:00	13:05	15:05
13. Jan			11:05	13:10
14. Jan	13:10	15:05		
15. Jan	11:00	12:55	12:55	14:55
16. Jan	12:55	15:25	11:00	13:00
17. Jan			11:05	12:55
18. Jan	13:15	15:00		
19. Jan	11:05	13:00	13:00	15:00
20. Jan	13:00	15:00	12:55	15:10
21. Jan	11:05	13:00	12:55	15:10
22. Jan	11:00	13:00	13:05	15:05
23. Jan			11:20	12:5
24. Jan			N/A	N/A
25. Jan	11:00	13:00	N/A	N/A
26. Jan	11:00	13:10	N/A	N/A
27. Jan			N/A	N/A
28. Jan	13:05	15:00	N/A	N/A
29. Jan	11:30	13:00	N/A	N/A
30. Jan	11:30	13:00	N/A	N/A
31. Jan	13:05	15:00	N/A	N/A

Table E.1: Times of photo sessions at Koala Encounter.

Appendix F

Mammal species at Koala Walkabout

Source if not stated otherwise: Ronald Strahan (2002) "The Mammals of Australia"
Pictures by Ingo Weidig

Quokka – *Setonix brachyrus*, Short-tailed Wallaby or Short-tailed Pademelon; Macropididae, Diprodontia, Marsupialia; head and body length 400 – 540; weight 2.7 – 4.2 kg.

The natural distribution range of the quokka is in southern West-Australia and on Rottnest Island, so this species is not conspecific to the koala. Quokkas are able to survive in harsh, seasonally arid habitats with low vegetation and little potable water. They defend an individual space, but also form groups of 25-150 individuals. Breading can occur throughout the whole year. The mainland population declines since the European settlement in Western Australia, but remains high on Rottnest Island.

Common Brushtail Possum – *Trichosurus vulpecula*, Phalangeridae, Diprodontia, Marsupialia; head and body length 350 – 550 cm; weight 1.2 – 4.5 kg.

The Common Brushtail Possum is found in most areas of Australia and is the most common possum in cities. Being nocturnal, it spends its day in a den and forages for food. This arboreal marsupial feeds mainly on leaves and fruit, but is generally omnivorous. It is also commonly known to raid rubbish bins and is therefore common in parks (Lindsey 1998). The Common Brushtail shows a remarkable tolerance to plant toxins and is able to digest eucalypt leaves. The tail is prehensile, enabling the Common Brushtail to climb rapidly. Communications includes a variety of sounds which can be heard over longer distances.

Common Ringtail Possum – *Pseudocheirus peregrinus*, Pseudocheiridae, Diprodontia, Marsupialia; head and body length 300 – 350 mm; weight 700 – 1100 g.

The Common Ringtail Possum is common in gardens of the eastern mainland, but rarely seen due to its shy, strictly nocturnal habits. The days are spent in dreys, which are built in trees. It is a specialized leave eater, but also feeds on flowers (particularly eucalypt), fruits and insects. It is also able to digest eucalypt leaves. It is a vocal animal, though much less than the Common Brushtail.

Appendix G

Details of statistical analysis

Figures 3.7, 3.8 and 3.9: Average monthly time budgets in *Ken* and the females during the year: Repeated-measurement ANOVA between months

SAMPLE	Behaviour	N	χ^2	FG	p
Ken	Resting	332	2.383	11	0.008
	Feeding	332	9.756	11	0.000
	Locomotion	332	2.818	11	0.015
Females	Resting	332	2.669	11	0.003
	Feeding	332	9.350	11	0.000
	Locomotion	332	6.890	11	0.000

Table G.1

Figure 3.7, 3.8 and 3.9: Average monthly day:night ratio in *Ken* and the females during the year: Repeated-measurement ANOVA between months

SAMPLE	Behaviour	N	χ^2	FG	p
Ken	Resting	332	2.636	11	0.003
	Feeding	332	5.112	11	0.000
	Locomotion	332	3.410	11	0.000
Females	Resting	332	7.581	11	0.000
	Feeding	332	6.813	11	0.000
	Locomotion	332	3.495	11	0.000

Table G.2

Chapter 3.1.4: Feeding bouts at Koala Walkabout.
Number of feeding bouts per day: t-test
N_{male} = 84, $N_{females}$ 237, T = 1.459, df = 319, p > 0.5, n. sig
Duration of single feeding bout: Kolmogorov-Smirnoff-Z-Test
N_{male} = 520, N_{female} = 1392, Z = 2.744, p = 0.000

Figs 3.41, 3.42, 3.43 and 3.44: Average daily time budget and day:night ratio for all behaviours of the koalas at Koala Walkabout (Sydney), Duisburg Zoo and Vienna Zoo: Repeated-measurement ANOVA und Friedman ANOVA

Zoo	
Sydney	42
Duisburg	38
Vienna	42

Table G.3: Number of days

Group	Season	Behaviour	Test	N	χ^2	FG	p
Males	Summer	Resting	ANOVA	122	10.933	2	0.000
		Feeding	ANOVA	122	39.886	2	0.000
		Loc1	Friedman	122	37.459	2	0.000
		Loc2	ANOVA	122	10.297	2	0.000
		Loc3	Friedman	122	65,819	2	0.000
		on ground	ANOVA	122	41.722	2	0.000
Females	Summer	Resting	Friedman	122	17.869	2	0.000
		Feeding	ANOVA	122	46.885	2	0.000
		Loc1	Friedman	122	62.755	2	0.000
		Loc2	ANOVA	122	44.137	2	0.000
		Loc3	Friedman	122	30.950	2	0.000
		on ground	Friedman	122	76.181	2	0.000
Males	Winter	Resting	ANOVA	122	39.462	2	0.000
		Feeding	ANOVA	122	42.407	2	0.000
		Loc1	Friedman	122	11.372	2	0.003
		Loc2	ANOVA	122	7,895	2	0.001
		Loc3	Friedman	122	70.525	2	0.000
		on ground	ANOVA	122	68.624	2	0.000
Females	Winter	Resting	ANOVA	122	6.337	2	0.002
		Feeding	ANOVA	122	24.658	2	0.000
		Loc1	Friedman	122	20.850	2	0.000
		Loc2	ANOVA	122	73.365	2	0.000
		Loc3	Friedman	122	44.293	2	0.000
		on ground	Friedman	122	68.624	2	0.000

Table G.4: Average daily time budget

Group	Season	Behaviour	Test	N	χ^2	FG	p
Males	Summer	Resting	ANOVA	122	11.233	2	0.000
		Feeding	ANOVA	122	14.494	2	0.000
		Loc1	Friedman	122	11.511	2	0.003
		Loc2	ANOVA	122	14.808	2	0.000
		Loc3	Friedman	122	14.309	2	0.001
		on ground	ANOVA	122	22.624	2	0.000
Females	Summer	Resting	ANOVA	122	8,736	2	0.000
		Feeding	ANOVA	122	47.145	2	0.000
		Loc1	Friedman	122	0.927	2	n. sig.
		Loc2	ANOVA	122	5.647	2	0.005
		Loc3	Friedman	122	15.753	2	0.000
		on ground	Friedman	122	???	2	???
Males	Winter	Resting	ANOVA	122	37.582	2	0.000
		Feeding	ANOVA	122	7.743	2	0.001
		Loc1	Friedman	122	20.307	2	0.000
		Loc2	ANOVA	122	35.217	2	0.000
		Loc3	Friedman	122	18.149	2	0.000
		on ground	ANOVA	122	58.696	2	0.000
Females	Winter	Resting	ANOVA	122	160.772	2	0.000
		Feeding	ANOVA	122	152.933	2	0.000
		Loc1	Friedman	122	6.274	2	0.043
		Loc2	ANOVA	122	73.365	2	0.000
		Loc3	Friedman	122	16.317	2	0.000
		on ground	Friedman	122	35.336	2	0.000

Table G.5: Average daily day:night ratio

Figure 3.45: Average duration of single feeding bouts, number of feeding bouts per day and average daily feeding time: Repeated-measurement ANOVA

Zoo	Number of feeding bouts	Number of days
Sydney	1912	168
Duisburg	2072	154
Vienna	1525	169

Table G.6: Number of feeding bouts and days

Average duration of single feeding bouts χ^2 = 567.42, FG = 2, p = 0.000

Average number of feeding bouts per day χ^2 = 149.75, FG = 2, p = 0.000

Average duration of total feeding χ^2 = 1637.88, FG = 2, p < 0.001

Figure 3.76: Average time budget and day:night ratio of females for different behaviours at Koala Walkabout and Koala Encounter: t-test

Zoo	N
Koala Walkabout	3
Koala Encounter	3

Table G.7: Number of females

SAMPLE	T	df	p $_{timebduget}$	p $_{day:nightratio}$
Resting	1.663	82	0.000	0.018
Feeding	1.663	82	0.000	0.000
Loc1	1.663	82	n. sig	n. sig
Loc2	1.663	82	n. sig.	0.026
Loc3	1.663	82	0.000	n. sig
on Ground	1.663	82	0.000	0.001

Table G.8: Average time budget and day:night ratio

3.7.3: Feeding bouts at Koala Walkabout and Koala Encounter

Number of feeding bouts per day: t-test

$N_{KoalaWalkabout}$ = 153, $N_{KoalaEncounter}$ = 168, T = -17.154, df = 319, p = 0.000

Number of feeding bouts per day: Kolmogorov-Smirnoff-Z-Test

$N_{KoalaWalkabout}$ = 707, $N_{KoalaEncounter}$ = 2006, Z = 2.476, p = 0.000

Figure 3.76: Average time budget for every behaviour with and without visitors during session time: t-test

Zoo	N
Day without visitors	11
Session 1	11
Session 2	11

Table G.9: Number of days

SAMPLE	T	df	p $_{Session1}$	p $_{Session2}$	p $_{complete24hours}$
Resting	2.306	8	n. sig.	n. sig.	n. sig.
Feeding	2.306	8	n. sig.	n.sig.	n.sig.
Loc1	2.306	8	n. sig.	n. sig.	n. sig.
Loc2	2.306	8	n. sig.	n. sig.	0.014
Loc3	2.306	8	n. sig.	n. sig.	n. sig.
on Ground	2.306	8	n. sig.	n. sig.	n. sig.

Table G.10: Time budget of all behaviours during session time with and without visitors

Acknowledgements

First of all, I'd like to thank my "Doktoreltern", Günther and Gerda Fleissner. They supported me when things started to fall apart and I had to find new ways for this PhD. Fleissners got me in contact with Ursula Munroe and somehow managed to find money from time to time to buy another camera.... We didn't always agree in the last six years, but they have never let me down.

Ursula Munroe has been a supervisor in everything but official name. Without her, I had never been able to make Australia come real. She gave me a place to stay in Sydney and was full of ideas and advice for the project. Thanks for all the discussion, the incredible help with the thesis and the papers and the stubbies after a hard day. And thanks for her four cats, who kept me company during months of video tape watching and cold Sydney nights.

Klaus Scheibe has heartily agreed to mark this thesis. Much more, he had some valuable advice for the manuscript, especially about animal well-being and protection.

I had a great time at Taronga Zoo, where Ken de la Motte and Erna Walraven gave me the chance to observe their koalas. The Oz Mammal team taught me a lot about koalas and koala husbandry, especially Annette Gifford, Christie Lombe and David Sharpe. They also gave me lots of hands-on experience with other marsupials and monotremes. Special thanks to Paul Davies for the time at the Nocturnal House. I also want to thank the technicians, especially Luke and Vince, who helped me to get all parts of the video system, set up everything and keep it running. I would have been lost without them.

Dagmar Schratter from Tiergarten Schönbrunn has been very supportive during my research, also her assistant Regina Pfistermüller, the senior koala keeper Simona Gabrisova. Herwig Pechlaner helped with the rather temperamental video equipment in Vienna. Tiergarten Schönbrunn kindly allowed me to use their video tapes for analysis.

Achim Winkler at Duisburg Zoo helped out with stud book data and lots of insider information on "koala politics". The keepers, Mario Kindemi and Siggi Lippmann were the first to teach me something about koala keeping and that they are not cuddly teddy bears (the koalas, of course!). They also changed video tapes for a full year and tried to help whenever the system stopped working.

Analysis ate up heaps of time and it would have been even more without the help of my boy-friend, Tronje Krop. He came up with several amazing computer scripts to plot ethograms and calculate time budgets, and he also developed the formula for the day:night ratio. Tronje helped me to layout this thesis and is responsible for me using Latex, not MS Word. We had heated discussion about math and stats, and most wondrously, our relationship survived them. I'm grateful that he was at my side.

I had the luck to be part of a fantastic research group, who supported me all the time. Very warm thanks to NCR! Special mentions to a couple of people:

Thomas Gbenro is our computer wizard and he's doing an awesome job! He came up with a great script to calculate power spectra, had unbelievable (and sometimes unrealisable) ideas for video observation systems, helped with all kinds of technical problems, was a scrutinizing proofreader and, last but not least, was a valuable person to discuss data with.

Christina Schubert has soldered several of the infrared-lights and had her very own way of labelling plus and minus (which drove Luke crazy and was responsible for fusing the video system at Koala Walkabout). We put together three video observation systems (including her "Moose TV") and had a moose of a time. Chris also was a reliable person to talk to when things got rough.

Claudia Kandler has been there all these years, did lots of proof-reading and simply was a great colleague to have around. She helped with setting up the equipment in Duisburg and was great organising conferences and workshops.

This project probably wouldn't have started without Joachim Scholz. He came up with heaps of ideas and advice, helped me with my applications for grants, was a great source for books on Australia and always had a very own view on koalas (which are politically uncorrect and will *not* be mentioned here). He also did some very helpful proof-reading.

Nini Henke took care of the video observation in Duisburg while I was in Australia. She was highly motivated and helped going through some of the video tapes. She and Ruben Holland de-installed the system in Duisburg. Tanja Ruch, Ursula Munroe and Semela Dukova helped with the statistics. (Any statistical mistakes in this study are completely *my* fault!) Friedhelm Krupp kindly advised me with my grant application. Michael

Melchinger helped with Adobe Illustrator, had some good ideas for graphics and never tired to offer help in the middle of the night.

There have been several proofreaders. Thanks to Thomas Gbenro, Christina Schubert, Claudia Kandler, Verena Kaspari and Florian Sicks for reading the English script and to James Ong for correcting all my mistakes in punctuations and style. Ilka Weidig did an amazing job with the last proof-reading and the printing. provided the printer for the first copies and kept me sane during a night of editing, reediting and printing.

Valuable scientific support on koalas was provided by Valerie Thompson and Jennifer Tobey from San Diego Zoo. Pearl Yusuf and Mark Rosenthal passed me some unpublished data on stress in koalas. There also have been many koala researchers and keepers I had the chance to discuss with.

During the whole PhD as well as during my studies before, my family supported me. Parts of the video system and my stay in Australia have been paid for by my grandparents, Anna Katharina and Günther Wolf. My parents, Andrea und Hans Benesch were always supportive and never stopped assuring me how proud they are. Warmest thanks to you all.

I'm very grateful to my friends, who cheered me up during the last years. And to my cat, you has the ability to calm me down by just sleeping next to me.

The first koala was handed to me by Christine Cooper. On that day I learned that koalas are very headstrong and loveable creatures. May they always get the respect they deserve and may they stay Australia's icon for a long time to come.

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List of Figures

List of Tables

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